Evolutionary food web models in fragmented landscapes

Evolutionäre Nahrungsnetze in fragmentierten Landschaften
Zur Erlangung des Grades eines Doktors der Naturwissenschaften (Dr. rer. nat.) genehmigte Dissertation von Diplom Physikerin Korinna Theresa Allhoff aus Iserlohn
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Erklärung zur Dissertation

Hiermit versichere ich, die vorliegende Dissertation ohne Hilfe Dritter nur mit den angegebenen Quellen und Hilfsmitteln angefertigt zu haben. Alle Stellen, die aus Quellen entnommen wurden, sind als solche kenntlich gemacht. Diese Arbeit hat in gleicher oder ähnlicher Form noch keiner Prüfungsbehörde vorgelegen.

Darmstadt, den 16.12.2014

(Korinna T. Allhoff)

Kurzzusammenfassung

Ökosysteme auf der ganzen Welt sind derzeit dramatischen Umweltveränderungen ausgesetzt. Die unmittelbare Folge davon sind erhöhte Aussterberaten. Nahrungsnetze, also Netzwerke von Räuber-Beute-Interaktionen, tragen zu einem grundlegenden Verständnis von Ökosystemen bei und unterstützen so die Identifizierung von sinnvollen Umweltschutzsmaßnahmen.

In dieser Arbeit untersuche ich evolutionäre Meta-Nahrungsnetze, also evolutionäre Netzwerke von Netzwerken. Die äußeren Netzwerke repräsentieren dabei fragmentierte Landschaften von mehreren Habitaten. Die inneren Netzwerke beschreiben lokalisierte Nahrungsnetze auf diesen Habitaten. Neue Spezies entstehen als Modifikationen von bereits extistierenden Spezies und die Populationsdynamik beschreibt, ob eine Spezies lebensfähig ist und wie sie mit anderen interagiert. Außerdem sind die Spezies in der Lage zwischen den Habitaten zu migrieren. Im Gegensatz zu früheren Arbeiten, die sich entweder auf räumliche oder auf evolutionäre Aspekte konzentrieren, berücksichtige ich beide und untersuche deren Zusammenspiel.

Ich benutze zwei verschiedene Modelle für die Beschreibung der lokalen Dynamik. Das erste Modell wurde 2005 von Loeuille and Loreau vorgestellt [1]. Es charakterisiert eine Spezies ausschließlich durch ihre mittlere adulte Körpergröße. Die entstehenden Netzwerke zeigen eine regelmäßige Struktur und sind bemerkenswert stabil. Meine Untersuchung diverser Modellvarianten zeigt, dass ein Modell zwei Bedingungen erfüllen muss um realistischere Netzwerke zu generieren. Einerseits muss eine Spezies durch mehr als eine Eigenschaft beschrieben werden und andererseits muss jede Eigenschaft auf einen realistischen Bereich beschränkt werden.

Basierend auf diesen Ergebnissen stelle ich ein neues Modell vor. Es ist weniger abstrakt als frühere Modelle, da alle Spezieseigenschaften eine klare biologische Bedeutung haben. Die Spezies werden durch ihre mittlere adulte Körpergröße, die Körpergröße ihrer bevorzugten Beute und die Breite ihres Beutespektrums charakterisiert. Die entstehenden Netzwerke zeigen viele unterschiedliche Strukturen von unterschiedlicher Größe und haben ein hohes Maß an Ähnlichkeit mit empirischen Daten. Die Artenzusammensetzung ändert sich ständig. Allerdings werden keine großen Aussterbelawinen, in denen mehr als 50% der Spezies aussterben, beobachtet. Dies legt die Schlussfolgerung nahe, dass solche Massenaussterbeereignisse in der Erdgeschichte externe Auslöser hatten.

Wenn man das Modell von Loeuille und Loreau auf mehrere Habitate erweitert, dann zeigen sich Ergebnisse, die bereits aus anderen Studien ohne Evolution bekannt sind. Erweitert man stattdessen das neue Modell um die räumliche Dimension, so ergibt sich ein viel breiteres Spektrum an Phänomenen. Indem ich die Migrationstärke, die Migrationsart und die räumliche Topologie variiere, zeige ich, dass die Kombination aus räumlichen und evolutionären Aspekten die Netzwerkstruktur und die Netzwerkstabilität anders beeinflusst als sie es einzeln tun

würden. Erst das Zusammenspiel liefert neue Erkenntnisse darüber, welche Faktoren Ökosysteme trotz ständiger Änderung der Artenzusammensetzung oder der räumlichen Umgebung stabilisieren.

Abstract

Ecosystems all over the world currently experience dramatic changes in their environment. The direct consequences are increased extinction rates. Food webs, which are networks of predator-prey interactions, provide a basic understanding of ecosystems and therefore help to identify reasonable conservation strategies.

In this thesis, I analyze evolutionary metacommunities, which can be modeled as evolutionary networks of networks: The outer networks represent fragmented landscapes of several habitats. The inner networks describe localized food webs on these habitats. New species emerge as modifications of existing species and population dynamics determines how the species interact and which species are viable. Additionally, species are able to migrate between the habitats. In contrast to previous studies that focus either on evolutionary or on spatial aspects, I include both and investigate the interplay between them.

I use two different evolutionary food web models to describe the local dynamics. The first model was introduced by Loeuille and Loreau in 2005 [1]. It characterizes a species by its average adult body mass, which is the only evolving trait. The resulting networks show a regular pattern and are remarkably stable. My analysis of several model variants reveals that a model has to fulfill two conditions to provide more realistic network structures: It should allow for the evolution of more traits in addition to body mass and it should restrict each evolving trait to realistic boundaries.

Based on these results, I introduce a new model. It is less abstract than earlier models of this type in the sense that all evolving traits have a clear biological meaning. The species are characterized by their average adult body mass, their preferred prey body mass, and the width of their potential prey body mass spectrum. The resulting networks cover a wide range of sizes and structures and show a high similarity to natural food webs. They exhibit a continuous species turnover. However, massive extinction waves that affect more than 50% of the network are not observed, suggesting that corresponding events in earth's history had external causes.

Metacommunities built with the model by Loeuille and Loreau show several results that are already known from non-evolving metacommunity studies. In comparison, metacommunities built with the new model show a much broader range of phenomena. By varying migration strength, migration type and spatial topology, I demonstrate that the combination of evolution and dispersal affects the structure and stability of food webs differently than each of them alone. The understanding of the interplay between evolution and dispersal leads to new insights into the factors that stabilize ecosystems despite changes in the spatial environment or the species composition.

Contents

1 Introduction

This chapter provides a theoretical background to my work. At first, I present a motivation and an overview of the different approaches that have already been taken in the analysis of ecosystems, see section 1.1 and 1.2. A brief overview of the structure and the key ideas of my thesis can be found in section 1.3.

1.1 Motivation

The complexity of ecosystems and the enormous biodiversity on earth has fascinated researchers for more than a hundred years now [2]. The interest in ecosystems exceeds simple curiosity, since human life is part of and depends on intact ecosystems. They provide us with food, resources and regulate our climate. Other examples of so-called ecosystem services are O_2-production, carbon storage, pollination, erosion control, storm protection and recreation [3].

Unfortunately, ecosystems all over the world currently experience dramatic changes in their environments. Human impacts can severely disrupt ecosystems, as shown for example in a recent study by Yeakel et al. [4]. The authors used historical information of species extinctions in order to reconstruct the collapse of an ecological network in Ancient Egypt. Climate change, habitat loss and habitat fragmentation due to agricultural land use has led to increasing extinction rates [5, 6], which could be harbingers of the sixth big mass extinction in earth's history [7, 8].

The loss of biodiversity due to disturbances in the environment is typically accompanied with a loss of ecosystem services [3]. The exact consequences of such a biotic crisis are difficult to predict, but certainly dramatic and likely to persist for millions of years [9]. Gaining a basic understanding of ecosystems, before irreversible collapses take place, is therefore of utmost importance in order to conserve these systems.

The focus of this thesis is on the influences of changes in the species composition and the spatial environment on the structure and stability of ecosystems. From a theoretical perspective, ecosystems can be described as food webs, which are networks of interacting species [10]. This network approach has many interfaces to theoretical physics. For instance, the analysis of extinction avalanches and the evolution of whole ecosystems is often based on methods from statistical physics [11]. The investigation of food webs provides insights into the structure and the dynamics of ecosystems. Food webs can thus help to predict their responses to changes in the environment or in the species composition.

1.2 Food webs as models of ecosystems

First, I would like to introduce some general ideas on food web analysis and some simple models, see subsection 1.2.1. In the following, I summarize the historical background of the diversity stability debate, see subsection 1.2.2. Recently, two new perspectives of food web analysis were introduced that include either evolutionary or spatial aspects, see subsections 1.2.3 and 1.2.4. The combination of both perspectives leads to the concept of evolutionary metacommunities, introduced in subsection 1.2.5, which is the major subject of my thesis.

1.2.1 What is a food web?

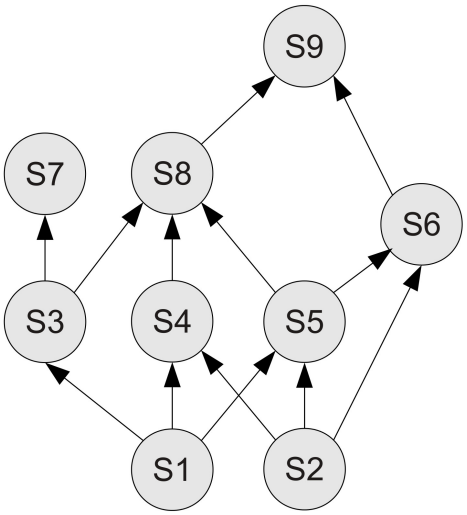

Figure 1.1.: Schematic food web of 9 species: The nodes represent species and the edges represent feeding links from prey to predator.

Food webs are models of ecosystems and describe them as networks of interacting species that focus on feeding relationships as the most important type of interactions [10]. Fig. 1.1 shows such a schematic food web, where the nodes represent species and the edges represent feeding links from prey to predator. The vertical position of a species represents its trophic position, which can be calculated in several ways. It indicates the number of times chemical energy is transformed from a consumer's diet into a consumer's biomass along the food chains that lead to the species [12].

References for several food web models can be found in the next subsection. Often, the population size of a species i is described via its biomass density B_i. The population dynamics can then be calculated via differential equations that capture the growth and loss terms due to predation, competition, respiration etc. A food web can hence be described by a set of coupled differential equations.

A simple approach for the population dynamics is to use Lotka Volterra equations:

$$\frac{dB_i}{dt} = B_i \left(b_i + \sum_j a_{ij} B_j \right), \tag{1.1}$$

where b_i is either a positive growth rate for basal species, or a negative death rate for other species, and where a_{ij} describes the interactions between the species [10]. The functional response in this approach is linear and does not depend on the biomass densities of predator or prey species. This simple approach hence does not account for predator saturation or predator interference. More realistic functional responses were discussed for example by Skallski and Gilliam in 2001 [13].

The network structure in most food web models is either extracted from empirical data or generated by some simple stochastic algorithm. One example of a model that provides such an algorithm is the cascade model [14, 15]. In this model, each species is characterized by an index i. With a constant probability, a predator species can prey on a species with a lower index. Preying on a species with a higher index is not possible. In comparison to the earlier studied random graphs, where each species can in principle prey on every other species, this cascading structure already covers several realistic patterns of food webs.

Another well-known model is the niche model by Williams and Martinez [16]. Similar to the cascade model, species are characterized by a "niche value" and hence sorted along the "niche axis". Additionally, a species is characterized by two more traits (feeding center and feeding range) that specify an interval on the niche axis. The species can hence consume those species that have a niche value within this interval. Prey species with similar niche values often share predators, leading to more realistic network structures. The feeding center of a species is typically smaller than its niche value. However, since its feeding range can exceed its niche value, the model allows for predation on prey species with higher niche values. This relaxes the strict hierarchy of the cascade model.

1.2.2 Historical background

The factors that stabilize food webs have been investigated since the seminal work by May in 1972 [17]. It suggested the conclusion that more complex food webs are less stable, which stands in contrast to observations in nature. This paradox is known as the diversity-stability debate [18]. However, it is criticized that May analyzed randomly constructed communities with randomly assigned interaction strengths.

Since then, various food web models have been introduced and many authors have shown that models for complex food webs can indeed be stable. This can be the case when empirically consistent food web topologies and interaction strength

distributions are used, as done by Yodzis [19], de Ruiter et al. [20] and Neutel et al. [21, 22]. Food webs can also be stable, when stability is not equated with dynamics going to a fixed point, but with species persistence, as for example investigated by Brose et al. [23], Williams and Martinez [24] and Kartascheff et al. [25].

Two important mechanisms were found to enhance the stability of food webs. The first is adaptive foraging, analyzed for example by Kondoh [26] and Uchida and Drossel [27]. It causes predators to turn away from prey species with a small population size and hence releases pressure on threatened species. The second mechanism are body-mass structures of larger species being on higher trophic levels than smaller ones. Larger animals have a slower metabolism than smaller animals so that the biomass flow reduces from lower to higher trophic levels. Such allometric effects have been analyzed for example by Brose et al. [23], Rall et al. [28] and Kartascheff et al. [29]. Both effects interact positively, so that the combination of both mechanisms leads to even more stable food webs, as demonstrated by Heckmann et al. [30].

The models mentioned so far capture many realistic properties of ecosystems. Nevertheless, like all models, they represent an idealization of real ecosystems. They consider a static species composition, ignoring temporal changes in the composition of the network due to species turnover. Moreover, they provide a mean field description, integrating the feeding relationships across the whole spatial extent of the system. However, introducing species turnover and spatial aspects into food web analysis leads to a wide range of new phenomena (or new explanations for already known phenomena), as summarized in the next subsections.

1.2.3 Introducing species turnover: Evolutionary food web models

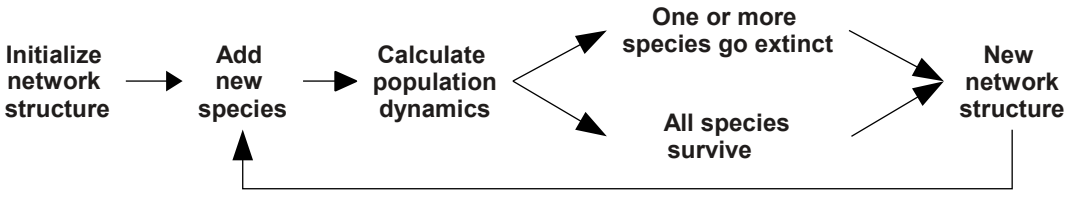

Figure 1.2.: Schematic algorithm of evolutionary food web models.

The food web structure in the models mentioned so far is imposed by hand and not emergent. However, real food webs are not produced by a generative algorithm, but have been shaped by their evolutionary history [31]. They show an ongoing species turnover: new species occur by immigration and speciation and other species vanish due to extinction. Yet, they are surprisingly stable in terms of long term persistence of the system as a whole.

Even without human interference or other catastrophic causes and apart from evolutionary suicide due to runaway selection [32], biological extinctions occur

due to intrinsic processes, i.e., the dynamic trophic and competitive interactions among species [33, 34]. The stability of food webs in terms of resistance to extinction waves after a perturbation (such as the removal or addition of a species), thus depends on the network structure of these interactions between the species [35]. Conversely, also the network structure results from species extinctions and additions. Understanding the interplay of food web structure and stability has therefore been identified as one of the most important questions in ecology [36].

A review on studies where evolutionary processes significantly affect the dynamics of populations, communities and ecosystems was presented by Fussmann et al. in 2007 [37]. Early attempts concentrated on the effect of co-evolution of two-species predator-prey systems. This work has been subsequently extended in order to study the eco-evolutionary dynamics of multi-species communities and the evolutionary emergence of whole ecosystems. During the last years, several models were introduced that include evolutionary dynamics as shown in fig. 1.2 in addition to population dynamics (see references below):

On a time scale much slower than population dynamics, new species, which are typically modeled as modifications of existing species, are added to the system. These new species can be interpreted either as invaders from another, not explicitly considered spatial region or as arising from a speciation process. If such a new species is able to establish itself in the network, it changes the environment for the already existent species in the sense that those species gain a new predator, prey or competitor species. These changes may threaten species that now experience a higher competition or predation pressure. Population dynamics then determines which species are still viable and which ones go extinct. Subsequently, also secondary extinction can occur, if a species loses one or more prey species.

The food web structure in such models emerges and evolves from the interplay between population dynamics and species addition. Evolutionary food web models give insights into the conditions under which complex network structures can emerge and persist in face of ongoing species turnover. They are thus fundamentally different from species assembly models, which have been studied for a longer time and which are based on a fixed species pool from which species are added to a smaller habitat.

The probably best studied evolutionary food web model with population dynamics is the webworld model [38, 39, 40, 41, 42], which bases the interaction between species on a vector of traits that can mutate. The model gives realistic network structures when adaptive foraging is included. Another model that uses trait vectors is the matching model [43], which was later extended to include population dynamics [44].

The extensive studies performed on the webworld model have shown that the emergence of complex food webs in evolutionary food web models is highly non-trivial and depends on the choice of the rules for population dynamics, as discussed by Drossel et al. [40]. Similar results were obtained in a study of an evolution-

ary version of the niche model [45], which allows for the evolution of three traits (niche value, center and width of feeding range) and produces complex, realistic food webs when allometric scaling and adaptive foraging are taken into account.

In 2005, Loeuille and Loreau [1] introduced the probably simplest successful evolutionary food web model. A species is specified by its body mass, which is the only evolving trait. The feeding and competition interactions are determined by differences in body mass. More examples of evolutionary food web models can be found in chapter 2, where I study the remarkable stability of this particular model, and in chapter 4, where I introduce a new model that is able to generate more realistic food web structures.

1.2.4 Introducing space: The metacommunity concept

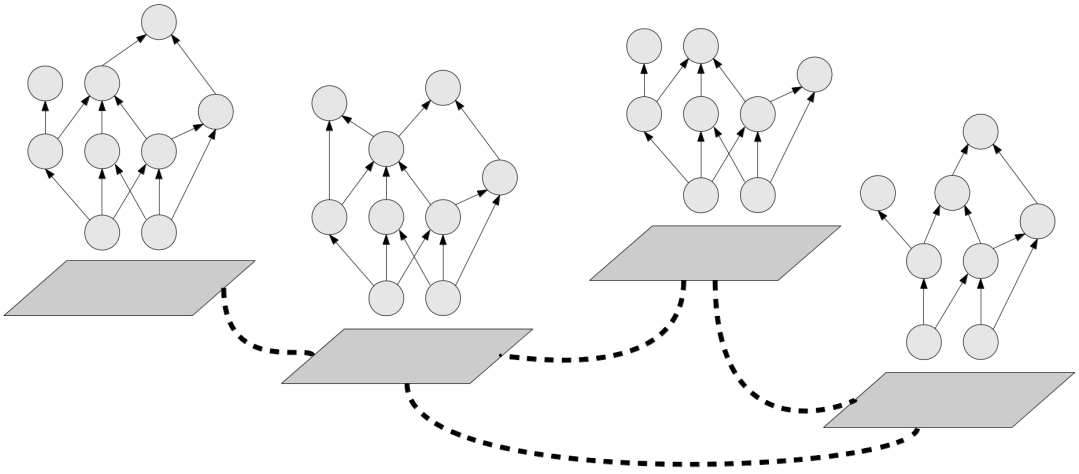

Figure 1.3.: Schematic metacommunity of four habitats coupled by migration links (dashed lines). The species are able to interact locally and to migrate between the habitats.

The evolutionary food web models presented in the previous subsection provide valuable insights into the emergence and the evolution of food web structure, but they typically fail to consider the influence of spatial aspects. However, an ecosystem is usually not an isolated system but coupled to other ecosystems. Recently, Bauer and Hoye reviewed the influence of migratory animals on the biodiversity and ecosystem functioning [46]. Those species cover remarkable distances in search for example for better feeding or reproduction environments. They interact trophically with the local species in several habitats as predator or prey species and hence represent a link between several ecosystems. Moreover, they can be carriers of nutrients, energy, toxicants, propagules, parasites etc. The examples summarized in the work by Bauer and Hoye highlight the need to include space into the analysis of food webs.

In order to go beyond mean-field models, various approaches have been taken to introduce space into food web models. If space can be described as discrete habi-

tats, one obtains "networks of networks". A schematic example of such a system is shown in fig. 1.3. The outer network represents the spatial landscape consisting of several habitats, whereas the connections between them represent possible routes for dispersal. A river with barrages results for example in a chain topology and a ring of habitats can occur along island shores. More complex spatial networks might represent archipelagos or a system of waterbodies connected by streams and canals. The inner networks describe localized food webs on these habitats, the connections between species representing feeding relationships.

The described networks of networks approach is known from other disciplines under many different names, as recently reviewed by Kivelä et al. [47]. However, in ecology, studies on such metacommunities are still underrepresented. The need to study spatially extended food webs has been highlighted not only by Bauer and Hoye [46], but also by several other authors [5, 6, 48, 49].

Most studies of spatial ecosystems concentrate on simple (non-evolving) topologies of the inner network, such as food chains [50] or small food web motifs of two [51, 52] or three [53, 54, 55, 56, 57] species in space. Ristl studied a diamond motif of four species [58] and found that the spatial topology of the outer network has a major impact on the robustness of the networks. A generalized modeling approach revealed a broad spectrum of different spatial effects, even when only a metapopulation of one single species is taken into account [59].

Single species and food web motifs are typically embedded in larger food webs. However, so far there exist only few investigations of larger food webs in space, both empirical [60, 61, 62, 63] and theoretical [64, 65, 66, 67, 68]. The analysis of large metacommunities deserves special attention, since it provides new insights into the diversity-stability debate. For example, Gravel et al. [69] observed complex food webs that were locally prone to extinction. Nevertheless, their complexity was observed to promote their persistence through regional dynamics. Pillai et al. also observed the emergence of complex food webs in space [70]. Their model considered complete competitive exclusion of inferior competitors from a given resource and within a given patch. The only way two species that potentially feed on the same resource can coexist within this patch is if one species is an omnivore and the other a generalist, here defined as feeding either on several trophic levels or on several patches, respectively. Therefore, very simple networks emerge locally, but complex networks can emerge through spatial aggregation of those local food chains.

1.2.5 Evolutionary metacommunities

The studies mentioned so far focus either on spatial aspects under the assumption that the species composition is static or on evolutionary dynamics and species turnover without considering space. Mooney and Cleland compiled a list of observed evolutionary consequences of the biotic rearrangements since the Age of

Exploration [71]. Immigration of alien species and changes in the spatial environment can thus be drivers of evolutionary processes. Real metacommunities therefore show a long-term behavior that can not be explained with the above mentioned metacommunity models. Also several other authors have emphasized that combining the spatial and the evolutionary perspective on ecosystems is essential for a better understanding of coexistence and diversity [61, 72, 73, 74, 75].

It is well known that including a spatial dimension in evolutionary models enables the coexistence of species or strategies that would otherwise exclude each other [76]. This is due to the formation of dynamical waves in which the competitors cyclically replace each other, or to the formation of local clusters that cannot easily be invaded from outside.

The persistence of species due to an interplay of evolution and dispersal was also observed in another study: Moya-Laraño et al. used an individual-based approach to study a metacommunity of 20 species in a patchy beech forest soil environment [77]. The authors varied the distance of the patches and the connectance of the local food webs. The study again highlights the urgent need to study the interplay between evolution and dispersal. However, evolution in this study affects only the 13 species traits that characterize the species, e.g. body size, sprint speed, metabolic rates etc. The emergence of new species according to speciation events and hence species turnover and the evolution of the food web as a whole is not taken into account.

The same holds for a study by Loeuille and Leibold, who introduced a metacommunity with two plant and two consumer species on twelve patches [78], where one of the plant species had evolving defense strategies. In two other evolutionary metacommunity studies, the same authors analyzed settings with changing local conditions [79] or with local negative feedback between the species and their environment [80]. These three studies by Loeuille and Leibold again provide results (e.g. the emergence of morphs) that arise from the interplay of evolution and dispersal and that would not occur in a setting where either evolution or dispersal is absent. More examples of evolutionary metacommunities will be discussed in chapter 3 and 5.

1.3 About this work

Up to now, studies on larger evolutionary metacommunities with many species on several trophic levels in complex spatial environments are extremely sparse. The goal of the present work is to fill this void. I extend the "network of networks"-approach explained in subsection 1.2.4 by including an evolutionary algorithm as explained in subsection 1.2.3. The results are "evolutionary networks of networks": Locally, species emerge, interact and go extinct according to an evolutionary food web model. Additionally, species are able to migrate between several habitats.

This work contains results from four independent studies. Each of these studies is represented in one chapter and the chapters are linked as follows.

Before building evolutionary metacommunities, it is at first necessary to understand the properties and capabilities of evolutionary food web models without spatial influences. My starting point is therefore the well-known evolutionary food web model by Loeuille and Loreau [1]. In chapter 2, I study the original model as well as several model modifications in order to identify the conditions which must be met to build a successful evolutionary food web model. The results from this first study play an important role in chapter 3, where I present results of evolutionary metacommunities using this particular evolutionary model to describe the local dynamics. The detailed knowledge about the original model helps to identify the effects driven by spatial influences and coming from an interplay between space and evolution.

The thorough investigations of this model and of model extensions show that it has several peculiarities. A more realistic evolutionary food web model is introduced in chapter 4. It is analyzed in detail and compared both to the first model and to empirical data. In contrast to the model by Loeuille and Loreau, it is able to produce networks with large extinction events and continuous species turnover. Therefore, its time dependent behavior (with and without space) shows a much broader spectrum of phenomena. In chapter 5, I present results of metacommunities built with this new evolutionary model. The focus of this study is on the question how the spatial coupling of food webs (for example when building canals between waterbodies) changes their diversity and functioning.

An overview of the results from these four studies can be found in chapter 6. There, also a collection of questions that arose from my work and led to further research topics can be found.

2 When do evolutionary food web models generate complex networks?

This chapter is based on results from my article "When do evolutionary food web models generate complex networks?". The article was co-authored by Barbara Drossel as my supervisor and published in the Journal of Theoretical Biology in 2013 [81].

In this study, I analyze the well-known evolutionary food web model by Louille and Loreau [1] as an example in order to discuss a rather general question: What is needed to build a successful evolutionary food web model? The knowledge about this particular model will be revisited in chapter 3, when discussing evolutionary metacommunities built with this model. The general insights into the emergence of complex networks will be used in the set-up of a new evolutionary food web model, see chapter 4.

2.1 Introduction

In subsection 1.2.3, an overview of serveral successful evolutionary food web models is given. However, the emergence of complex food webs in such models is highly nontrivial. Some past attempts to set up an evolutionary model lead to repeated network collapse instead of persisting complex networks [82]. Some authors avoid food web collapses by including a sufficiently large rate at which new species are introduced [83]. Other authors achieve complex networks only by including mutualistic interactions in addition to feeding interactions [84, 85], leading to complex networks dominated by mutualists. Other attempts lead to trivial network structures, like simple food chains in the evolving niche model [45] or a single trophic level in the webworld model [40]. In both models, adaptive foraging was required in order to obtain more complex networks.

Here, I re-evaluate the model introduced by Louille and Loreau [1]. It was introduced in 2005 and is probably the simplest successful evolutionary food web model. In contrast to other well-known models, like the matching model [43, 44] or the webworld model [38, 39, 40], which describe a species by a vector of many abstract traits, a species in this model is specified only by its body mass. This makes the model less abstract and easily comparable to empirical data. It therefore attracted considerable attention and was subsequently modified and extended by several authors. For example, a version with gradual evolution was studied by Brännström et al in 2011 [86]. Another recent extension of the model, which allows for the niche width to evolve in addition to body mass and thus produces a larger variety of networks than the original model, was suggested in 2009 by Ingram et al. [87].

Remarkably, the original model generates stable food web structures of various sizes that show many realistic network properties - despite its simplicity and despite the fact that it does not include two prominent features considered important for food-web stability, namely adaptive behavior and full allometric scaling of growth and loss terms with body mass.

The purpose of this chapter is to investigate the reasons for this remarkable stability in order to get a better understanding of what is generally necessary in evolutionary food web models to generate complex networks. For this purpose, I study the original model (section 2.2) as well as various modifications concerning changes in the population dynamics and in the evolutionary rules (section 2.3). In particular those modifications that allow for evolutionary changes of the center and the width of the feeding range in addition to the evolution of body mass can lead to dramatic changes in the resulting network structures. The results suggest that it is essential to constrain the evolution of these quantities such that neither extremely well adapted specialists nor generalists with extremely broad feeding ranges can occur, or, if they occur, usually fare worse than intermediate species and can therefore not become established.

Finally, in section 2.4, I discuss the implications of our findings and argue that the conditions that stabilize other evolutionary food web models (e.g. adaptive foraging or allometric scaling) have similar effects. They also prevent the occurrence of extreme specialists or extreme generalists that in general have a higher fitness than species with moderate feeding parameters.

2.2 The original model by Loeuille and Loreau

In the following, the original model is introduced and some typical simulation runs are presented. The simulations presented here have the purpose to provide a basic understanding of evolving food webs. A quantitative analysis of the resulting network structures can be found in chapter 4, where this model will be revisited and compared to the new evolutionary model.

2.2.1 Model description

The model by Loeuille and Loreau [1] includes population dynamics on the one hand and the introduction of new species via modification of existing species on the other. Because such "mutation" events are very rare, population dynamics typically reaches an attractor before the introduction of a new species. Thus, ecological and evolutionary time scales can be seen as separate.

Here and in the following chapter I use the nomenclature introduced by Loeuille and Loreau for better comparision with their original work. Note that it differs from the nomenclature used to describe the new model in chapter 4 and 5.

Population dynamics is based on the body mass x_i of a species $i \in \{1, ..., n\}$ as its only key trait. Species are sorted such that body mass increases with index number. Production efficiency f and mortality rate m scale with body masses according to the allometric relations $f(x_i) = f_0 x_i^{-0.25}$ and $m(x_i) = m_0 x_i^{-0.25}$. The population dynamics of species i with biomass density N_i is modeled by

$$\begin{aligned} \frac{dN_i}{dt} &= f(x_i) \sum_{j=0}^{i-1} \gamma_{ij} N_i N_j && \text{(predation input)} \\ &- m(x_i) N_i && \text{(mortality)} \\ &- \sum_{j=1}^{n} \alpha_{ij} N_i N_j && \text{(competition)} \\ &- \sum_{j=i+1}^{n} \gamma_{ji} N_i N_j && \text{(predation loss) .} \end{aligned} \tag{2.1}$$

The function γ_{ij} in eq. (2.1) is a Gaussian function describing the rate with which predator i consumes prey j. A predator can only consume prey with a smaller body mass than its own. The most favored prey has a body mass difference d to the predator. The standard deviation s of the Gaussian is a measure of the degree of specialization:

$$\gamma_{ij} = \gamma(x_i - x_j) = \frac{\gamma_0}{s\sqrt{2\pi}} \exp\left(\frac{-(x_i - x_j - d)^2}{s^2} \right) . \tag{2.2}$$

The function α_{ij} in eq. (2.1) describes the interference competition between species with similar body masses and hence similar feeding preferences. Its strength is $\alpha_{ij} = \alpha(|x_i - x_j|) = \alpha_0$ if $|x_i - x_j| \leq \beta$, and zero otherwise.

Note that the feeding parameters d and s do not depend on the body mass and have the same value for all species. Since this Gaussian consumption rate is in principle infinitely large, one has to introduce a cutoff criterion for links that are too weak to be regarded as existent. Loeuille and Loreau used a threshold of 15% of the maximum attack rate in their analysis. The cutoff rule is irrelevant for the investigations in this chapter, but will be revisited in more detail in chapter 4.

Energy input into the system is provided by an external resource of "body mass" $x_0 = 0$ and total biomass N_0. This resource grows according to a constant input of inorganic nutrient I and decreases due to an outflow eN_0, in addition to being consumed by the other species. Furthermore, the resource increases due to the re-

cycling of a proportion ν of the biomass loss implied in the expressions for mortality, competition and predation,

$$\frac{dN_0}{dt} = I - eN_0 - \sum_{i=1}^{n} \gamma_{i0} N_i N_0 + \nu \sum_{j=1}^{n} m(x_i) N_i + \nu \sum_{i=1}^{n} \sum_{j=1}^{n} \alpha_{ij} N_i N_j + \nu \sum_{i=1}^{n} \sum_{j=0}^{i-1} \left(1 - f(x_i)\right) \gamma_{ij} N_i N_j \,. \tag{2.3}$$

Starting from a single ancestor species of body mass $x_1 = d$, the food web is gradually built up by including evolutionary dynamics in addition to the population dynamics. A new species is introduced with a "mutation" rate of 10^{-6} per unit mass and unit time. If a mutation occurs in population i, the new species has a body mass drawn randomly from the interval $[0.8x_i, 1.2x_i]$. The initial biomass density of a mutant is also the extinction threshold for all species. So only mutants with a positive growth rate can add successfully to the system, those with negative growth rate go extinct immediately.

I used the C-language and the Runge-Kutta-Fehlerberg algorithm provided by the GNU Scientific library [88] to perform my computer simulations. I chose all parameters as in the original work by Loeuille and Loreau except for the initial biomass density, which was increased to 10^{-6}. This has no influence on the general results, but allows for a lower computational accuracy and therefore faster calculations. Simulations are typically run for a total time of $2 \cdot 10^8$ units or longer. For comparison, the generation time of a species with body mass $x_i = 2$ and $m_0 = 0.1$ is of the order of $\frac{1}{m(x_i)} = \frac{x_i^{0.25}}{m_0} \approx 12$ time units. In the realizations of the model, generation times between 1 and 20 time units occurred.

2.2.2 Typical simulations

In their original article, Loeuille and Loreau demonstrated that their model is able to produce a large variety of robust networks, depending on the model parameters. They identified the niche width s and the competition strength α_0 as the most important parameters that affect the structure of the networks. When the niche width s is smaller and when the competition strength α_0 is smaller, the trophic levels are more distinct, as can be seen from their fig. 2 and their evaluation of the trophic structure. Furthermore, the statistical analysis in their fig. 3 shows that while the total biomass remains approximately constant if α_0 is not too small, the number of species increases with increasing α_0 and increasing niche width s. The chain length and thus the number of trophic levels is not very sensitive to the two parameters, if α_0 is not too small.

My own computer simulations confirm these observations. These trends are illustrated in the pictures of the resulting food web structures shown in fig. 2.1.

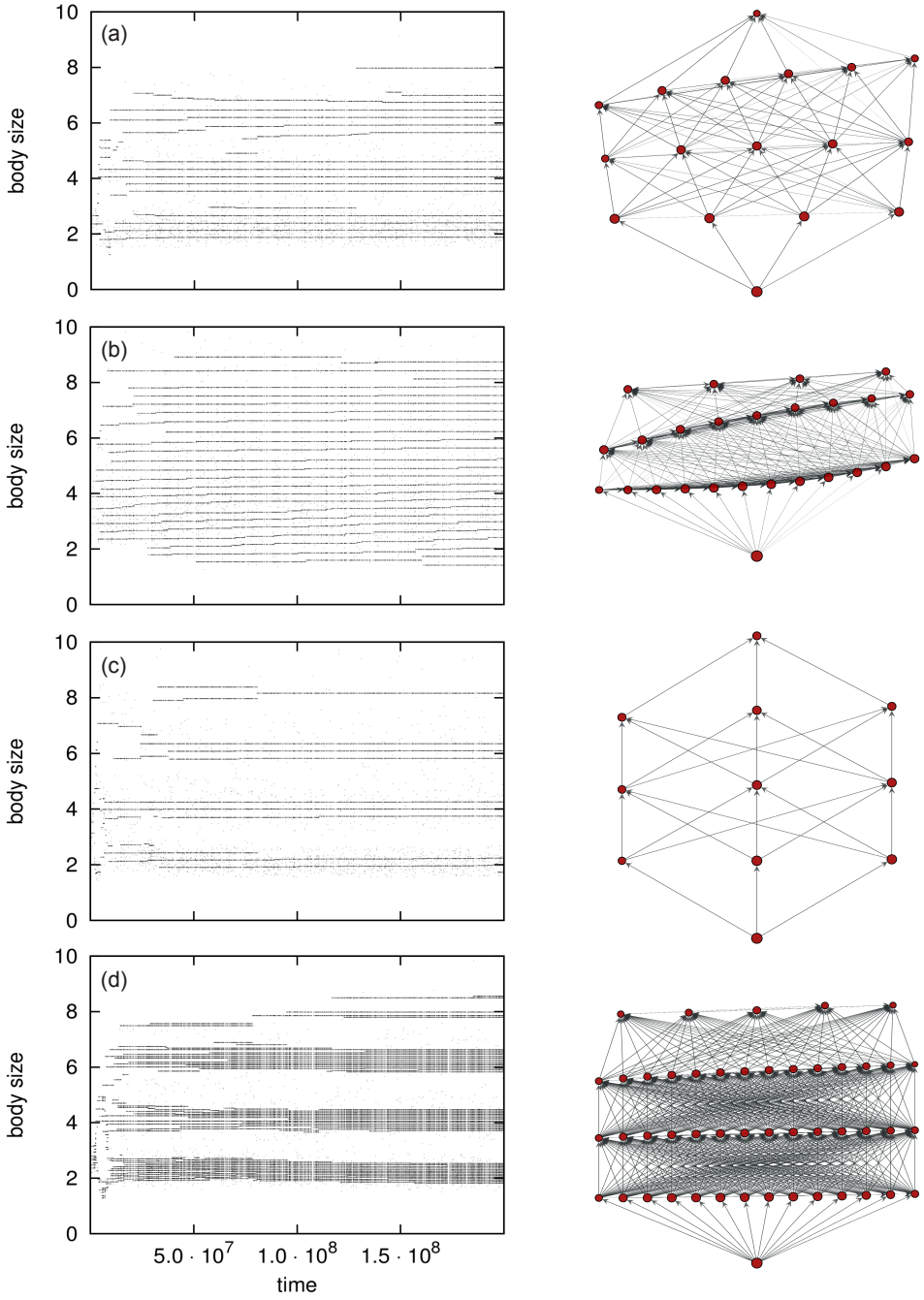

Figure 2.1.: Evolution of body masses and corresponding networks after $2 \cdot 10^8$ time units generated with the model by Loeuille and Loreau [1]. Vertices represent species, with the radius scaling logarithmically with population size. Arrows point from prey to their predator, with the width scaling logarithmically with the consumption rate. The vertical position of a species in the network represents its flow-based trophic position, which is the averaged weighted position of the prey plus one [12]. Parameter values: $f_0 = 0.3$, $m_0 = 0.1$, $\gamma_0 = 1$, $d = 2$, $I = 10$, $e = 0.1$, $\nu = 0.5$; (a): $s^2/d = 1/2$, $\alpha_0 = 0.1$, $\beta = 0.25$; (b): $s^2/d = 5/2$, $\alpha_0 = 0.1$, $\beta = 0.25$; (c): $s^2/d = 1/2$, $\alpha_0 = 0.02$, $\beta = 0.25$; (d): $s^2/d = 1/2$, $\alpha_0 = 0.1$, $\beta = 0.05$. Network visualizations here and in the following are based on *graph-tool* (http://graph-tool.skewed.de).

If the feeding range is narrow ($s < d$), only species with body masses that are approximately a multiple of d find enough prey to survive. These species with $x \approx l \cdot d$ consume those with $x \approx (l-1) \cdot d$. They have a trophic position of approximately $l+1$, if the resource represents the first trophic level. Subfigures (a), (c) and (d) show this pronounced trophic level structure. For larger feeding range s, species feed from a broader range of prey and the trophic levels merge, as shown in subfigure (b).

The competition strength α_0 has an important influence on the resulting network since it limits population sizes. Smaller values of α_0 imply larger populations and therefore less populations on a given trophic level (see subfigure (c)), because the energy provided by the resource can support only a certain total biomass. In agreement with Loeuille and Loreau, I found that with no competition at all, $\alpha_0 = 0$, the network structure is chain-like.

In addition to s and α_0, also the competition range β plays an important role, see subfigure (d). To avoid competition, species keep a minimum body mass difference of β, allowing for more species on a trophic level when β is smaller. This is consistent with a mean field calculation performed for a similar model by Lässig et al. [89].

The network visualizations in fig. 2.1 illustrate the trends to merging levels with increasing s and to more species with increasing α_0 or decreasing β. They also demonstrate the capability of the model to reproduce statistical properties of a broad variety of empirical food webs. However, these pictures also reveal unrealistic features of the model:

In all cases examined, the network consists of a few (typically three or four) trophic levels above the resource, each with a few species feeding on all those in the level below and being eaten by all those in the level above. The body mass difference between the levels equals approximately the feeding distance d, and the body mass difference between the species is not smaller than the competition range β. Species with body masses very close to a multiple of d are in the center of a trophic level. They have the best feeding conditions and hence the largest population sizes compared to other species of the same level. This regular, uniform structure, which is clearly visible in fig. 2.1, is due to the fact that species differ by only one trait and have the same values of the feeding parameters d and s and the competition parameters α_0 and β.

In our simulations we also observed that species turnover is very low. Once such a structure has emerged, it persists over time without further changes. After the network has reached its final structure only small changes occur, where a species is replaced by a slightly different one, and no other species goes extinct subsequent to the creation of the new species. Due to the regular, predictable network structure, larger changes of the network cannot occur.

A modification of this model where the niche width s can evolve within certain limits was introduced by Ingram et al. [87] . It produces less uniform networks that

contain omnivores and specialists. The level of omnivory turned out to be higher when the range over which the niche width varies is larger. The authors found that in this case the species turnover is also faster and the temporal fluctuation in species number is larger.

2.3 Model variants

In order to identify the factors that are responsible for the high stability and regularity of the model by Loeuille and Loreau, I present several model versions with changes in the population dynamics (subsection 2.3.1) and in the evolutionary rules (subsection 2.3.2).

2.3.1 Modified population dynamics

In other evolutionary food web models, the emergence of complex network structures depends on various features of the population dynamics equations, such as allometric scaling and adaptive behavior [40, 45]. In order to test to what extent this is also the case in the model by Loeuille and Loreau, I modified the population dynamics in several ways.

Loeuille and Loreau already noted that replacing the linear functional response by a Holling type II term, which accounts for predator saturation, does not change the qualitative results and I confirm this observation. Ingram et al. [87] also replaced the box-shaped competition function with a Gaussian and they reported no changes in the model behavior. Furthermore, I investigated a version of the model without allometric scaling, setting the production efficiency and the mortality rate to constant values $f(x_i) = f_0$ and $m(x_i) = m_0$. The change in the results is negligible. This is at first sight surprising, since it is known that allometric scaling has a considerable stabilizing effects on food web dynamics. However, a closer consideration reveals that even in the original model by Loeuille and Loreau allometric scaling has barely any influence, because all body masses x_i in this model are in the range of $2 \leq x_i \leq 8$. The factors by which the production efficiency and the mortality rate vary between species are thus in the small interval from $8^{-0.25} \approx 0.60$ to $2^{-0.25} \approx 0.84$.

Finally, I deactivated the recycling loop in the equation for the resource (2.3). This modification simply decreases the total amount of available biomass in the system. However, just like the previously mentioned modifications, it does not affect the main mechanism outlined in the previous subsection that species within the same trophic level are spaced at a distance β on the body mass axis, and that the distance between trophic levels is around d.

All these findings mean that the food web structure produced with the model by Loeuille and Loreau is robust with respect to modifications of the population dynamical rules. In contrast, the evolutionary rules have a strong influence on the

structure and stability of the model. In the next subsection, I show that a change of the evolutionary rules such that the feeding distance d and the feeding range s can evolve, destroys the robustness of the model.

2.3.2 Modified evolutionary rules

In order to relieve the strong constraint that all species have identical parameter values (apart from body mass), I studied a version of the model where the feeding parameters d and s can evolve, so that each species obtains its own feeding distance d_i and its own feeding range s_i. This model version is similar to the evolutionary niche model [45], which also allows for the evolution of three parameters that determine the feeding relationships.

If a mutation occurs in population i, the new traits s_j and d_j of the mutant population j are drawn randomly from an interval of size ± 10 % around the traits of the parent species i. Its body mass x_j is drawn randomly from an interval of size ± 20 % around x_i, as before. With these modifications, the consumption rate is now

$$\gamma_{ij} = \frac{\gamma_0}{s_i\sqrt{2\pi}} \exp\left[-\left(\frac{x_i - x_j - d_i}{s_i}\right)^2\right]. \tag{2.4}$$

With this change, the body masses of the species are no longer restricted to small multiples of the feeding distance d, as explained in subsection 2.2.2. In particular, species with big body masses can be viable if their feeding distance d_i is also large, so that species with much smaller body mass are within their feeding interval. Thus, the possible body masses span a much wider range and I therefore made the competition range β dependent on body mass, $\alpha(|x_i - x_j|) = \alpha_0$ if $|x_i - x_j| < 0.1 \cdot \max(x_i, x_j)$. Otherwise, the competition range would be negligible for species with big body masses, leading to competition only between conspecifics and to the coexistence of unrealistically large numbers of species with big body masses.

Again, all simulations started with a single ancestor feeding on the external resource. Parameter values given in the caption of fig. 2.1 remained unchanged or served as initial values (except for β). The new mutation rules lead to longer simulation times, which made it necessary to increase the mutation rate to 10^{-5}. This is still rare enough that population dynamics typically reach an attractor before the next mutation occurs.

Two evolving traits

At first, I analyzed the influence of the two new evolving traits separately. With constant predator-prey-distance $d_i = 2$ for all species but individual feeding ranges

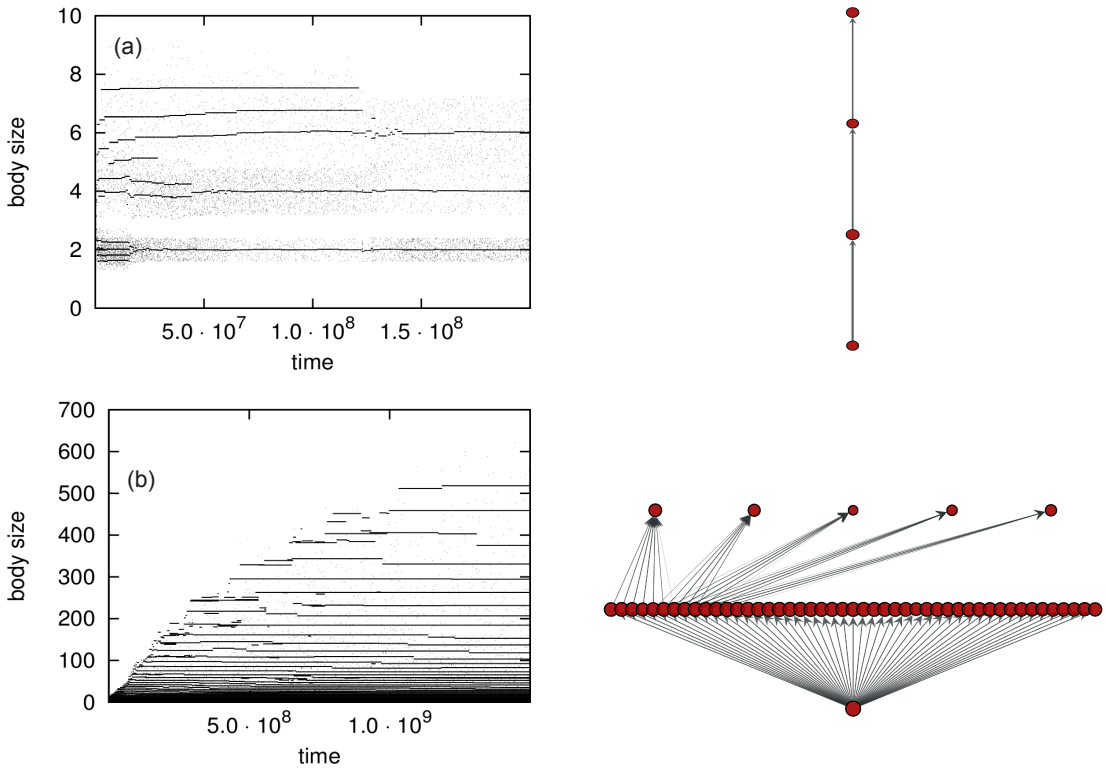

Figure 2.2.: Evolution of body masses with the modified model by Loeuille and Loreau, where either s_i or d_i evolve in addition to the body mass x_i. Parameter values given in fig. 2.1 remain unchanged or serve as initial values (except for β, see subsection 2.3.2). (a): The evolving traits are the body mass x_i and the feeding range s_i. (b): The evolving traits are the body mass x_i and the predator-prey distance d_i.

s_i (fig. 2.2 (a)), only species with body masses of d, $2d$, $3d$ etc have a chance to survive the initial simulation stages. This is because highly adapted specialists with small s_i, that have a body mass that is larger by $d_i = 2$ than the body mass of their prey, obtain more energy from their prey than less adapted species with a larger feeding range. Therefore, s_i evolves towards zero. Competition then leads to only one species per trophic level and the food web becomes a simple food chain.

These simulations are similar to the case $c = 0$ in the model version studied by Ingram et al [87], and the authors report indeed that in the case $c = 0$, where there is no preferred feeding range s_0, food webs that are complex collapse eventually, with all species going extinct. But they do not observe simple food chains, probably because the Holling type 2 functional response limits the population sizes of perfectly adapted predators so that generalists can evolve.

In the opposite case, where feeding ranges are constant, $s_i = 1$ for all species but predator-prey distances d_i evolve (fig. 2.2 (b)), the regular network structure observed with fixed d_i is destroyed. Now every species with a suitable predator-prey distance, regardless of its body mass, can be viable. Those species feeding on the external resource have clear advantages against higher level species, because their direct link to the resource provides a large energy input that cannot go extinct.

This leads to a network structure where many species with a considerable range of body masses feed exclusively on the resource and where only very few second level species occur.

We conclude that when either s_i or d_i evolves, simple network structures emerge, and the previously observed complex structures cannot occur any more.

Three evolving traits

When both parameters are allowed to evolve, the final network structures are again simple, with only a few species feeding on the resource. However, evolution can go through complex intermediate stages before the final structure is obtained. An example of a simulation run is shown in fig. 2.3. After an initial period of strong diversification a network with approximately 25 species persists for a long time until most species suddenly disappear in an extinction avalanche at $t \approx 2.4 \cdot 10^8$. To explain this, I analyzed the network structures of this specific run at different stages of the evolutionary process. Other simulation runs are similar, although of course the precise moments in time at which transitions occur differ between simulations.

Like in the original model, the network emerges from a single ancestor species. Examples for complex intermediate network structures are also shown in fig. 2.3. Some predators are already highly specialized on a single prey, whereas others are omnivores and have several but weaker links to their prey. The dominating trend during evolution is a decreasing width of the feeding range (decreasing value of s_i), which implies an increase of the maximum consumption rate. Just as in the case where only s_i evolved and d_i was fixed, specialists have an advantage over omnivores and even over other, less adapted specialists. Thus, the omnivores become replaced with time and the links in the network get fewer and stronger. A broom-like structure with well adapted species emerges. This structure can be interpreted as a combination of the results of the two cases where only one of the feeding parameters evolves, see fig. 2.2. The variable predator-prey distance causes a species-rich second trophic level, whereas the variable feeding range favors the emergence of specialists and hence of food chains. The "hairs" of the broom eventually collapse to a length of 1 because a predator can lose its prey when the prey species gets replaced by a mutant. At $t \approx 1.5 \cdot 10^6$ all remaining species in the system are highly specialized on the resource and no higher trophic levels are occupied.

In this situation, a small body mass implies a high production efficiency and therefore a big population size and a high probability to mutate. Consequently, after the collapse to only one trophic level, the body masses tend to become ever smaller. This may lead to problems, if the production efficiencies become larger than 1. However, since this process is very slow, it is not shown in fig. 2.3.

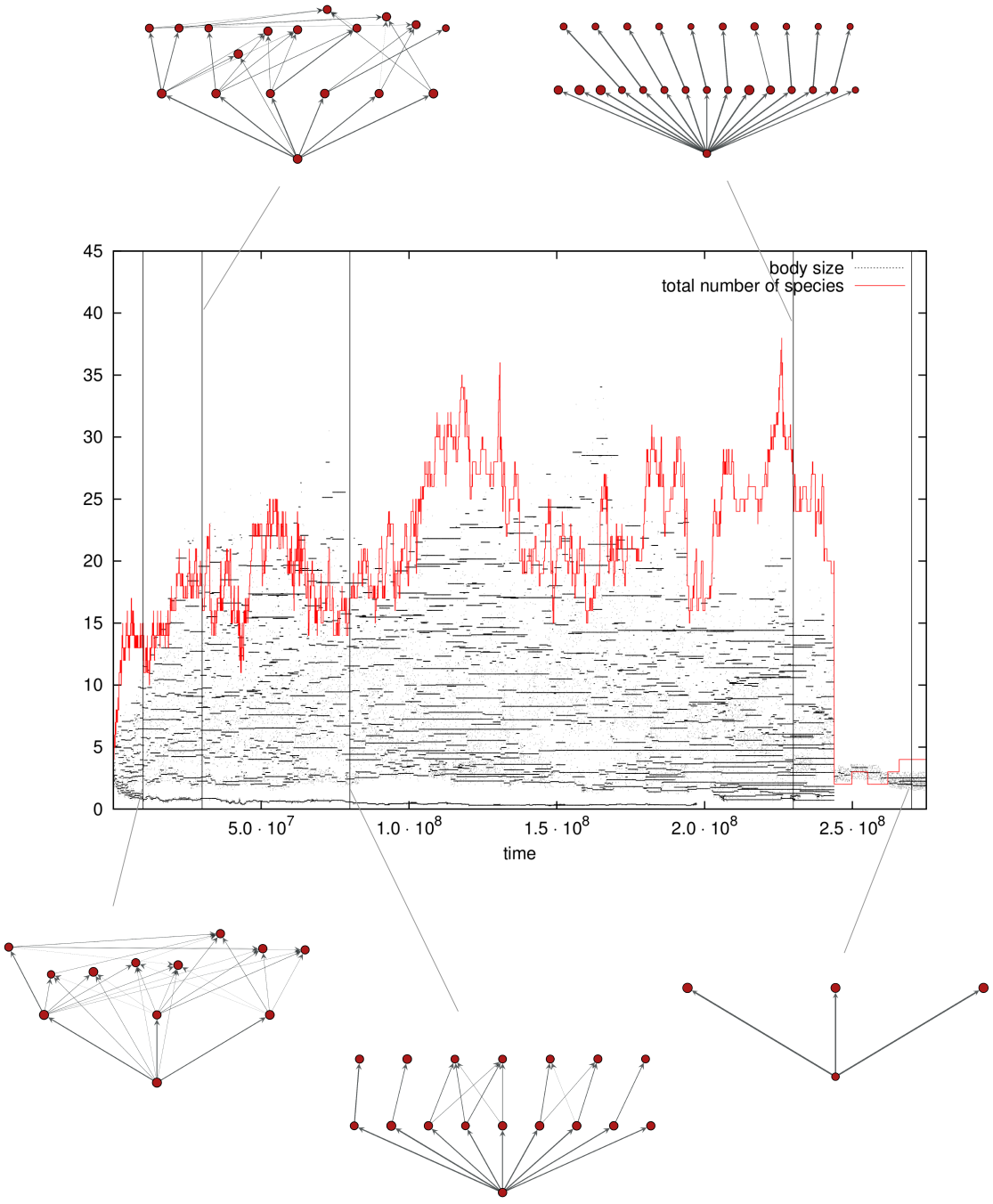

Figure 2.3.: Evolution of body masses with the modified model by Loeuille and Loreau where s_i and d_i evolve in addition to x_i. Parameter values given in fig. 2.1 remain unchanged or serve as initial values (except for β, see subsection 2.3.2). The network structures correspond to the time points indicated by vertical lines. A transient complex structure emerges from a single ancestor species.

In the model version with a fixed competition range $\beta = 0.25$, mutants of species with small body masses are automatically in the competition range of their parent species and go extinct immediately, so body masses are restricted downwards. In a model version where each species is chosen to become a parent species of a mutant with the same (biomass independent) probability, the trend to ever smaller body masses does not occur either.

As a final investigation, I tried to prevent the emergence of ever more specialized predators by studying a scenario where the maximum consumption rate is fixed and only the width of the Gaussian function evolves,

$$\gamma'_{ij} = \frac{\gamma_0}{\sqrt{2\pi}} \cdot \exp\left[-\left(\frac{x_i - x_j - d_i}{s_i} \right)^2 \right] . \tag{2.5}$$

Now, omnivores receive a clear advantage because the feeding range can be in principle arbitrarily wide and include arbitrary many prey species. The resulting networks are dominated by species with ever larger body mass and with feeding ranges as large as their own body mass, so that they are able to consume all smaller species and the resource. As a consequence, small species with few prey have more and more predators and go extinct eventually.

This unrealistic phenomenon can be avoided by introducing foraging efforts according to

$$\gamma_{ij} = \frac{\gamma'_{ij}}{\sum_{j=0}^{i-1} \gamma'_{ij}} \cdot \gamma'_{ij} . \tag{2.6}$$

This approach is analogous to the ideas of the evolutionary niche model [45]. However, now specialists win again because they have the largest feeding rate on a given prey and the result is again a broom-like structure.

These investigations suggest that constraining the feeding distance d and the feeding range s is an essential requirement for preventing unrealistic evolutionary trends in a model where both these parameters can evolve.

2.4 Discussion

The original model by Loeuille and Loreau with the body mass as the only evolving trait (section 2.2) produces very stable networks. Some ecological properties of these networks, such as the total number of species or the number and distinctiveness of trophic levels, can be changed significantly by varying the appropriate parameter values. However, the investigations presented in this chapter show that all networks generated by the model have the same underlying uniform structure, due to the facts that all species have the same feeding distance d and the same feeding range s and that interspecific competition has the same range for all species. Even

if a newly emerging species is slightly better adapted to the resources and therefore displaces a species of similar body mass, it has the same feeding preferences and hence the same function in the food web so that secondary extinctions can not occur.

More complex and realistic networks would contain generalists with rather wide feeding ranges and specialists with rather narrow feeding ranges. In order to enable these, it is necessary to allow for evolving feeding parameters d and s. The idea of introducing more evolving traits in addition to body mass is also consistent with results from an empirical study by Rall et al [28], who found that predators of similar body mass can differ significantly in their feeding preferences and survival strategies. The dimensionality of food webs, i.e. the question how many traits are required to predict whether two species interact, has also been discussed recently by Eklöf et al. [90], who suggested that a rather small number of traits (≤ 6 in 196 of 200 analyzed networks) is already sufficient to completely explain all interactions in a food web. This is at odds with previous evolutionary food web models (e.g. the webworld model [38, 39, 40, 41, 42] or the matching model [43, 44]), which characterize a species via a vector of many abstract traits.

Unfortunately, the same mechanism that produces the uniform structures in the model by Loeuille and Loreau is also responsible for the remarkable robustness of the model. By individualizing d and s this mechanism is destroyed and unrealistic trends occur. Complex structures can emerge transiently, but are no longer persistent. In the realization presented in section 2.3.2, specialists get so superior that the network finally collapses. A similar situation occurs in the evolutionary niche model [45], too. The authors observed the same broom-like structure as shown in fig. 2.3 when the model did not contain adaptive foraging.

Our study shows that it is essential to restrict every evolving trait in order to avoid unrealistic trends such as ever smaller body masses or ever narrower or broader feeding ranges. Indeed, a closer look at those evolutionary models that successfully generate complex food webs shows that they all include in one way similar restrictions.

For example, in the original model by Loeuille and Loreau, the body mass is kept within narrow limits through the fixed predator-prey distance d, combined with the small number of trophic levels that are possible in food webs due to the energy loss from one level to the next. This limitation of the evolution of body mass is still the case in the recent extension of the model analyzed by Ingram et all [87]. Similar to our study (see fig. 2.2), the feeding range s evolves in addition to the body mass. The tendency towards ever narrower specialists is avoided by introducing an optimum value s_0 of the feeding range. Species with significantly differing values of s_i have lower attack rates and are therefore less viable. This naturally constrains the range over which s_i can evolve and allows for the emergence of complex food webs.

The evolutionary niche model studied by Guill and Drossel [45] produces complex food webs when adaptive foraging efforts are included. A predator is then able to invest the main effort in its most profitable prey without becoming dependent on it. Links to alternative prey are weaker or inactive and can be increased if the most profitable prey species declines. This prevents the evolution of extremely narrow specialists. On the other hand, the evolution of extremely broad omnivores is also prevented, because the strength of competition between two species depends on the overlap in their feeding ranges. Competition terms that depend only on the body mass, as in the model by Loeuille and Loreau, cannot prevent very broad generalists, unless foraging efforts are included (e.g. by dividing the attack rates by the number of prey species of a predator) so that their typical rate of food intake does not increase with the number of prey species.

Similarly, the webworld model leads to complex network structures when adaptive foraging is included [39, 40], and it also contains a competition term that depends on the prey overlap. Interestingly, the webworld model was shown to produce complex networks even without adaptive foraging when the feeding rates were modified such that only the "best" predators could feed on a given prey [40]. The emergence of very specialized predators in this version of the model is probably prevented by the fact that species are characterized by many traits and that feeding relationships are determined from a large matrix of scores between traits. As a result, there exist neither species that can only feed on one other species nor does decreasing the number of prey lead to a better efficiency at using these prey.

Including allometric scaling in the evolutionary niche model [45] in addition to adaptive foraging resulted in a larger number of trophic levels. This is due to the slower flow of biomass to higher trophic levels, allowing more species to coexist on these levels. It can therefore be expected that the number of species and levels would also increase in the model by Loeuille and Loreau if allometric effects were fully included, in particular if the trait values x_i did correspond to the logarithm of the body mass instead of the body mass.

In summary, we found that a successful evolutionary food web model requires two things: On the one hand, the evolutionary rules must allow for the evolution of more than one trait, for instance the feeding ranges s_i and feeding distances d_i in addition to the body masses x_i. This allows for the emergence of a variety of different feeding strategies observed in nature, such as specialists or omnivores, and furthers the creation of realistic networks with variable and complex structures. On the other hand, the model must include restrictions for each evolving trait in order to prevent the emergence of unrealistic trends. Two possibilities to achieve this goal are 1) including costs for large deviations from the preferred parameter values, as discussed by Ingram et al, and 2) including adaptive foraging and a competition strength that depends on niche width as done in the webworld model and the evolutionary niche model.

3 Evolutionary metacommunities I

In this chapter, I present results from the article "On the interplay of speciation and dispersal: An evolutionary food web model in space". The article was co-authored by Eva Marie Weiel, Tobias Rogge and Barbara Drossel and published in the Journal of Theoretical Biology [91]. The main idea of this study is to use the evolutionary food web model by Loeuille and Loreau [1] as a starting point to build evolutionary metacommunities. In contrast to many previous studies that focus either on evolutionary or on spatial aspects, we include both and investigate their interplay.

In the previous chapter I identified several peculiarities of the original, non-spatial model. However, the fact that its evolutionary behavior is already well understood helps to identify and to understand the effects arising from the spatial topology. In order to discuss the generality of the results of this study, I later compare them to results from less static evolutionary metacommunities built with a more realistic model, see chapter 5.

The results shown in this chapter were computed using a C-Program, which is based on the program that I developed for the study presented in the previous chapter. It was subsequently extended by Eva Marie Weiel and Tobias Rogge in order to contain dispersal between several habitats. Several figures in this chapter are based on results from the master thesis of Eva Marie Weiel (2013) [92]. Tobias Rogge performed the simulations of the chain topology presented in subsection 3.3.2 in the context of his bachelor thesis in 2013 [93]. I myself wrote the final article, reevaluated the simulations performed by Eva Marie Weiel and performed many additional simulations with intermediate migration rates for the figures in subsection 3.2.3.

3.1 Introduction

As mentioned in subsection 1.2.5, studies on large evolutionary metacommunities are sparse, although several authors have highlighted their importance. A study with four species was published in 2008 by Loeuille and Leibold [78], who investigated a food web model with two plant and two consumer species on a patchy environment. The environment consisted of twelve patches differing in the amount of nutrient they provide for the plant species. One of the plant species had evolving defense strategies. The authors demonstrated the emergence of morphs that could only exist in a metacommunity due to the presence of dispersal, highlighting the fact that the combination of space and evolutionary processes yields important new insights.

In two other metacommunity studies, Loeuille and Leibold also considered a changing local environment [79] and negative feedback between the species and their local habitat [80]. However, all three studies are simplified in the sense that only one species has evolving traits ignoring any co-evolutionary effects [78], or that population dynamics and trophic interactions are not taken into account [79, 80] or that each habitat is occupied by only one single species [80].

In this chapter, more complex evolutionary metacommunities consisting of large food webs with several trophic levels are introduced. We use the model by Loeuille and Loreau [1], placing it on several habitats that might represent lakes, islands or a fragmented landscape and that are coupled by migration. Locally, the species emerge, interact and go extinct according to the rules of the original model. Additionally, species are able to migrate between the habitats. The results are "evolutionary networks of networks".

In a first step, we analyze a simple scenario of diffusive dispersal between two homogeneous habitats in order to get a basic understanding of such evolving metacommunities, see section 3.2. In a second step, we extend this scenario by considering a more complex migration type or more complex spatial topologies, see section 3.3. By varying the migration rules (undirected, directed, diffusive, adaptive or dependent on body mass), the time of migration onset (at the beginning or after the local food webs have evolved), and the number and properties of habitats (2 or 8 habitats, equivalent or differing with respect to simulation parameters), we investigate many different scenarios.

With diffusive migration, our results agree qualitatively with diversity-dispersal relationships from empirical studies [94] and from other theoretical metacommunity studies [66, 67, 73]. Low migration rates lead to an increased diversity in the local habitats, and high migration rates lead to homogenization of habitats and hence to a decreased regional diversity. For a chain of eight habitats coupled by diffusive migration, we find that migration leads to equal biomasses in the habitats, even when the species composition of neighboring patches is very different. With adaptive migration, we observe species compositions that differ considerably between patches and contain species that are descendant from ancestors on both patches. This result indicates that the combination of spatial aspects and evolutionary processes affects the structure of food webs in different ways than each of them alone.

3.2 Diffusive dispersal between two homogeneous habitats

To describe the emergence of new species as well as feeding and competition interactions that take place on a local habitat, we use the evolutionary model as explained in section 2.2.1. Compared to the original model, only the dispersal link between the habitats needs to be introduced.

3.2.1 Modeling dispersal

We chose a simple diffusion approach to describe migration between two equivalent habitats. Each species can have two populations, one on each habitat. For each population of species i on each habitat h we add a migration term to equation (2.1):

$$\dots - \underbrace{\mu_{i,h\to h'} N_{i,h}}_{\text{migration from } h \text{ to } h'} + \underbrace{\mu_{i,h'\to h} N_{i,h'}}_{\text{migration from } h' \text{ to } h} \qquad \left[h, h' \in [1,2],\ h \neq h'\right] \tag{3.1}$$

Here, $\mu_{i,h\to h'}$ and $\mu_{i,h'\to h}$ are the migration rates of species i. We do not include loss terms, which means that all biomass leaving one habitat appears on the other. The resource is supposed to be confined to its habitat and does not migrate, $\mu_{0,h\to h'} = \mu_{0,h'\to h} = 0$.

We consider diffusive migration, where the migration rates are treated as constants $\mu_{i,h\to h'} = \mu$ for all h, h', i with $\mu \in \left(10^{-1}, 10^{-2}, ..., 10^{-6}\right)$. We also investigate the variant with directed migration, for which $\mu_{i,h\to h'} = 0$ if $h' > h$. For high values of μ, dispersal occurs on a similar time scale as population dynamics; for instance the mortality rate of the ancestor species with $x_1 = 2$ is $m_0 x_1^{-0.25} \simeq 0.085$. Moreover, we investigate the case of allometrically scaled migration rates, $\mu_{i,h\to h'} = \mu_{i,h'\to h} = \mu \cdot x_i$, where species with larger body masses migrate faster.

All these cases are analyzed in two versions. In the first version, the migration rates are zero during the initial build-up of the networks. Migration sets in only after the networks have fully emerged. This mimics situations in which separate ecosystems become coupled, for example by the building of canals between waterbodies, or by the formation of land bridges. In the second version, migration sets in at the beginning of the simulation so that both habitats co-evolve. We also discuss the case where migration is switched off after some time.

In systems with migration, the extinction threshold must be treated differently than in the original model. Due to emigration, the biomass of new mutants can initially fall below the extinction threshold, even when the new species is viable. Therefore, we first apply population dynamics after each "mutation", and only after the new population equilibrium is reached, species that are below the extinction threshold are removed. Interestingly, population dynamics always went to a fixed point, we never saw periodic oscillations or chaotic attractors.

If not indicated otherwise, we use a fixed set of parameters ($d = 2$, $\frac{s}{d} = 0.5$, $f_0 = 0.3$, $m_0 = 0.1$, $\gamma_0 = 1$, $\alpha_0 = 0.1$, $\beta = 0.25$, $I = 10$, $e = 0.1$, $\upsilon = 0.5$) in order to concentrate on the effects generated by the spatial landscape. These parameter values correspond to the original values introduced by Loeuille and Loreau. With this parameter set, networks of approximately $16 - 18$ species emerge. As in the

previous chapter, we use an initial biomass density of emerging species of 10^{-6}. Simulations were usually run for $4 \cdot 10^8$ time units (with the original mutation rate of 10^{-6}) or for $2 \cdot 10^7$ time units (with an increased mutation rate of $2 \cdot 10^{-5}$). This allows for faster calculations without influencing the results, since the population dynamics still acts on a much faster timescale.

We repeated all simulations several times in order to make sure that the results are generic. In the most intensely studied case of diffusive migration between two equivalent habitats, we performed more than 450 simulation runs.

3.2.2 Two typical outcomes

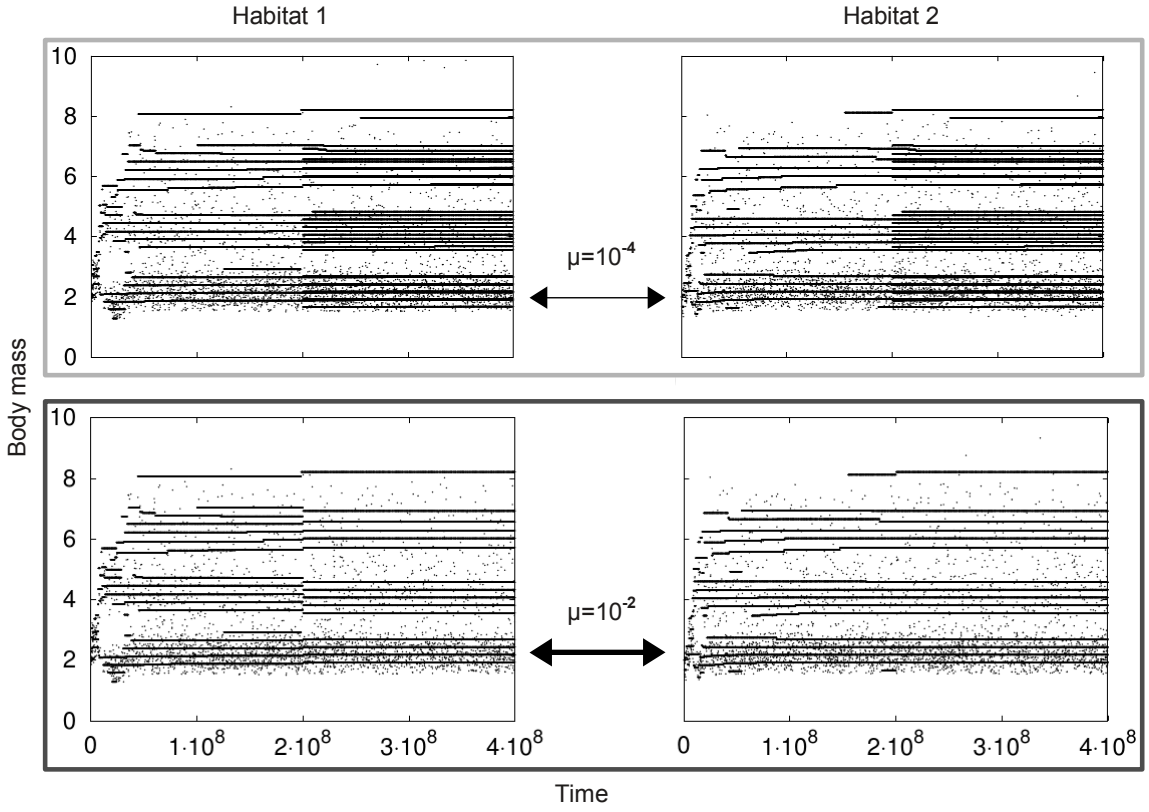

Figure 3.1.: Evolving body masses in two habitats, simulated with the model by Loeuille and Loreau [1]. Migration between the habitats with $\mu = 10^{-4}$ (top line) or $\mu = 10^{-2}$ (bottom line) starts at $t = 2 \cdot 10^8$ after the initial build-up of the networks. The resulting networks are shown in the top line of fig. 3.2. (Based on results from Eva Marie Weiel [92]).

Starting from a single ancestor species, the evolutionary model by Loeuille and Loreau [1] goes first through a period of strong diversification, and then the network structure stabilizes and assumes a regular pattern. Fig. 3.1 shows the body masses of all species occurring during two exemplary simulations in two habitats that are initially isolated. Predator species with a body mass of $x_i \approx l \cdot d$ consume prey species with a body mass of approximately $(l-1) \cdot d$. Hence, those predators

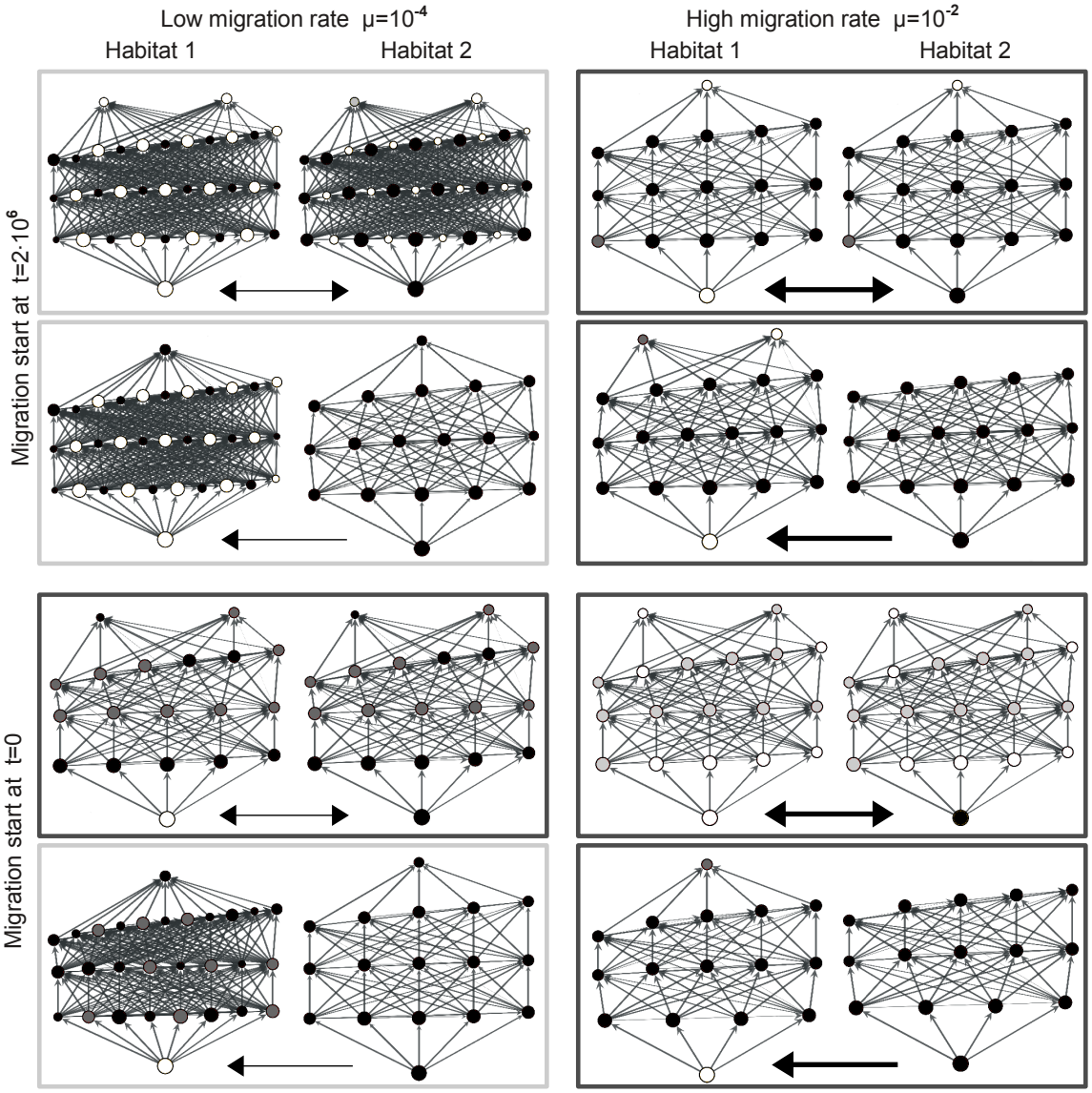

Figure 3.2.: Example networks on two habitats coupled by weak (left panels) or strong (right panels) migration. The arrows between the networks indicate the direction of migration. The vertices represent species, with the radius scaling logarithmically with biomass density, and the arrows between species represent feeding links. The colors of the species represent their habitat of origination: White (black) species are natives of habitat 1 (2) and originated there, too. Light (dark) gray species originated in habitat 2 (1), but are descendants of a white (black) species. The vertical position of a species represents its trophic position, which is the average, weighted trophic position of its prey, plus one ("flow-based TL" [12]). Time evolution of the networks in line 1 is shown in fig. 3.1. The color of the frames around the networks indicates the two possible outcomes. Light gray frames: networks with small additional populations (outcome 1). Dark gray frames: similar / identical networks (outcome 2). (Based on results from Eva Marie Weiel [92]).

have a trophic position of approximately $l + 1$, if the resource represents the first trophic level. To avoid competition, species keep a minimum body mass difference of β, allowing for more species on a trophic level when β is smaller [81]. The competition in this model is exclusive: If two species are so similar in body mass that they compete with each other (e.g. parent and mutant species), then only one of them survives. Although the realizations in the two habitats are based on the same set of parameters, they show slightly different structures due to different sets of random numbers.

At time $t = 2 \cdot 10^8$, undirected diffusive migration between the two habitats according to equation (3.1) sets in. Dependent on the migration rate, two major outcomes can be identified, which are here and in the following marked by a light or dark gray frame:

Outcome 1: For small migration rates (e.g. $\mu = 10^{-4}$, see top line in fig. 3.1), migrants have small additional populations in the foreign habitat, leading to an approximately doubled number of species per habitat. The resulting network structures are thus combinations of the isolated networks.

Outcome 2: In case of a high migration rate (e.g. $\mu = 10^{-2}$, see bottom line in fig. 3.1), native species become displaced by invaders. The resulting networks are very similar or even identical in the two habitats.

In both cases, the outcome is reached soon after the onset of migration. Since the immigrants arrive in a habitat where the network is already completely developed, every niche is already occupied and all immigrants have to compete with native species. If migration rate is small, the immigrants' gain in biomass due to migration and feeding interactions becomes soon canceled by competition losses, and the immigrant populations stay small. As soon as migration is switched off, these small populations vanish again (not shown). With a higher migration rate, some immigrants can establish themselves against their competitors and displace native species. Again, all species (invaders and natives) tend to keep a body mass difference of $\geq \beta$ to minimize their competition loss. Since all species from one habitat and especially from one trophic level co-evolved together, they are in this respect well matched to each other. As a consequence, often complete levels are replaced.

In fig. 3.2, the resulting network structures of several simulation runs are shown. The first line corresponds to the simulations shown in fig. 3.1. The colors of the species represent their habitat of origin. White species are natives to habitat 1 and black species are natives to habitat 2. If a black species migrates into habitat 1 and has a mutant there, this mutant is colored dark gray. Light gray species have analogously originated in habitat 2 but are descendants of a white species from habitat 1.

We also analyzed scenarios where migration is only allowed into one direction or where migration starts at the beginning of the simulation. Directed migration (fig. 3.2, line 2) leads to similar results for the immigration habitat as undirected migration. The network structure in the emigration habitat depends on the migration rate. The migration loss can be formally regarded as an increased mortality term for all species in habitat 2. In case of very low migration rates, this term is negligible and leaves the network structure of habitat 2 unchanged. In case of high migration rates, a significant amount of biomass leaves the emigration habitat per unit time, leading to the extinction of one or more species from the upper levels.

If undirected migration starts at the beginning of the simulation (fig. 3.2, line 3), both resulting networks are identical and only either black and dark gray or white and light gray species occur. The first successful mutant that replaces its ancestor species in its home habitat is also able to migrate to the other habitat and displace also the ancestor's population there. Every subsequent mutant is a descendant from this first mutant and finds identical conditions in both habitats, leading to identical networks.

Line 4 of fig. 3.2 shows results of directed migration during the whole simulation time. We observe a combination of the explained effects. All species are descendants of the first successful invader from habitat 2 and therefore either black or dark gray. For a low migration rate, we observe again small additional populations in habitat 1 (outcome 1). For a high migration rate, the networks are mostly identical (outcome 2) except for the top level.

3.2.3 Intermediate migration rates

In order to gain a general overview of the influence of the migration rate, we varied its value over several orders of magnitudes, $\mu \in (10^{-1}, 10^{-2}, ..., 10^{-6})$ and performed a total number of 48 simulations. Larger or smaller migration rates influence the time needed until the system reaches a new fixed point after a mutation event, but the resulting network structures do not provide any new insights besides the two explained outcomes. Intermediate migration rates lead to a superposition of the two outcomes, where one trophic level contains additional small populations corresponding to outcome 1 and another trophic level is replaced by species from the other habitat corresponding to outcome 2.

We observed essentially the same effect for body-mass dependent migration rates, with the migration rate being proportional to the body mass (another 120 realizations, data not shown). Since species on higher levels had larger migration rates, they were more often replaced, while lower levels showed more often additional populations. However, since in this model all body masses are of the same order of magnitude, body-mass effects are only minor.

To understand the transition from small to large migration rates in more detail, I performed more than 400 simulation runs with $2 \cdot 10^{-2} \geq \mu \geq 7 \cdot 10^{-5}$. Fig.

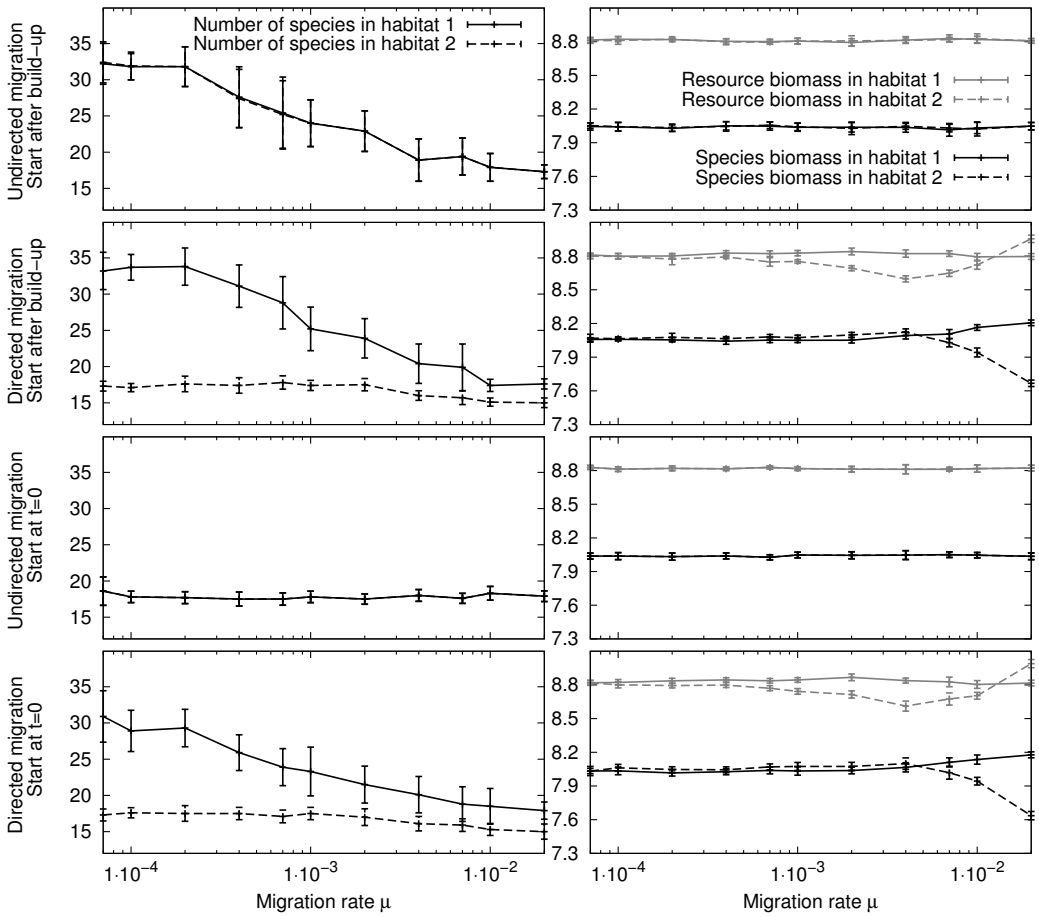

Figure 3.3.: Network size and total biomasses of resources and all other species in dependence of the migration rate μ. Each data point represents the average and standard deviation of 10 simulation runs with different random numbers. Isolated habitats show the same results as realizations with undirected migration starting at the beginning of the simulation (line 3).

3.3 shows a smooth transition between the described two outcomes that covers approximately two decades of the migration strength μ. With undirected migration starting after the initial build-up (line 1), each species has populations in both habitats so that the number of species per habitat is identical. In case of a high migration rate, not only the species number, but the whole networks are identical (outcome 2), whereas in case of a rather small migration rate, the network size is approximately doubled due to small additional populations (outcome 1). However, even if the species composition strongly depends on the migration rate, the total biomasses of the resources and the total biomass of the species do not (see top line of fig. 3.3). It is even nearly identical for both habitats and shows very small variations across the realizations that differ only in the set of random numbers.

The situation is different with directed migration (fig. 3.3, line 2). The number of species in habitat 1 shows a similar smooth transition from many additional populations to the displacement of native species, whereas habitat 2 accommodates a rather constant number of species. Only in case of high migration rates,

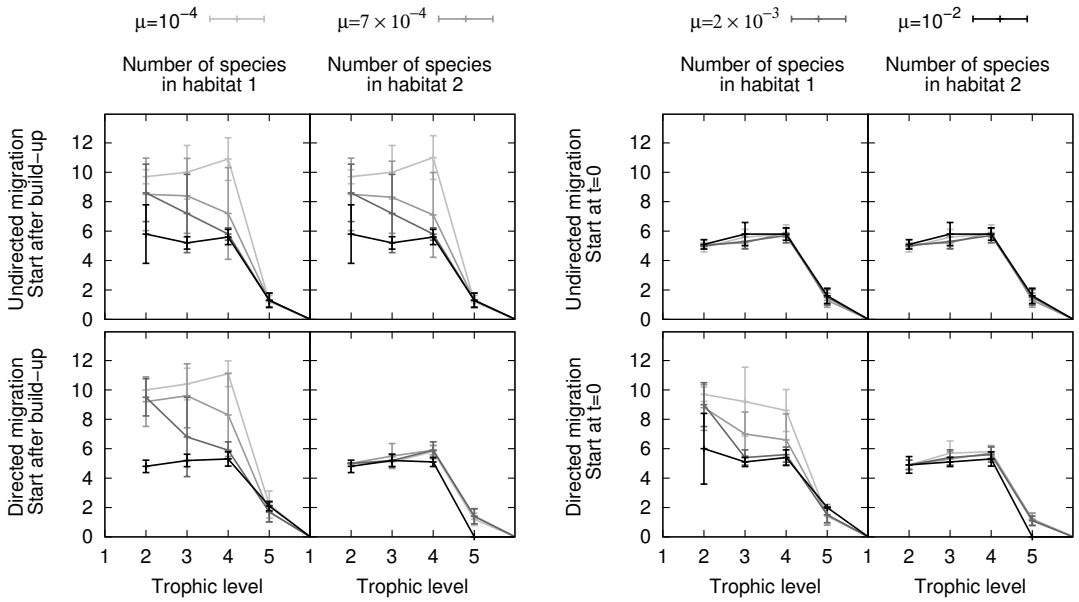

Figure 3.4.: Number of species per trophic level (rounded to nearest integer values) for simulations of 4 different scenarios and for 4 values of the migration rate μ. The resource represents the first trophic level. Each data point represents average and standard deviation of 10 realizations with different random numbers. Isolated habitats show the same distribution as realizations with undirected migration starting at the beginning of the simulation (top right panel).

species from upper trophic levels become extinct due to the migration losses, as explained above. This leads to a non-monotonous dependence of the biomasses on the migration rate, according to the following top-down trophic cascade [95]: For $\mu \approx 3 \cdot 10^{-3}$, all species in the fifth trophic level of habitat 2 are extinct due to migration losses, so that species in the fourth level experience no predation pressure. Hence, even despite their own migration losses, they can have big populations and exert a high pressure on the third level. Due to the subsequent reduction of population sizes in the third level, species in the second level also experience a reduced predation pressure, have big populations and exert a high pressure on the first trophic level, which is observed as a reduced resource biomass. For even higher migration rates, also species from the fourth level in habitat 2 become extinct due to migration losses, the total biomass of the species decreases and the resource recovers.

If undirected migration starts at the beginning of the simulation (fig. 3.3, line 3), identical networks emerge, as explained above. The results do not depend on the migration rate and are identical with results from simulations of isolated habitats (not shown). If directed migration is active during the build-up of the networks (fig. 3.3, line 4), we observe in principle the same effects as when migration sets in after the initial build-up. However, some immigrants occasionally find an empty niche as long as the build-up is not yet completed. They do not have to compete with natives and can establish themselves, reducing the number of additional small

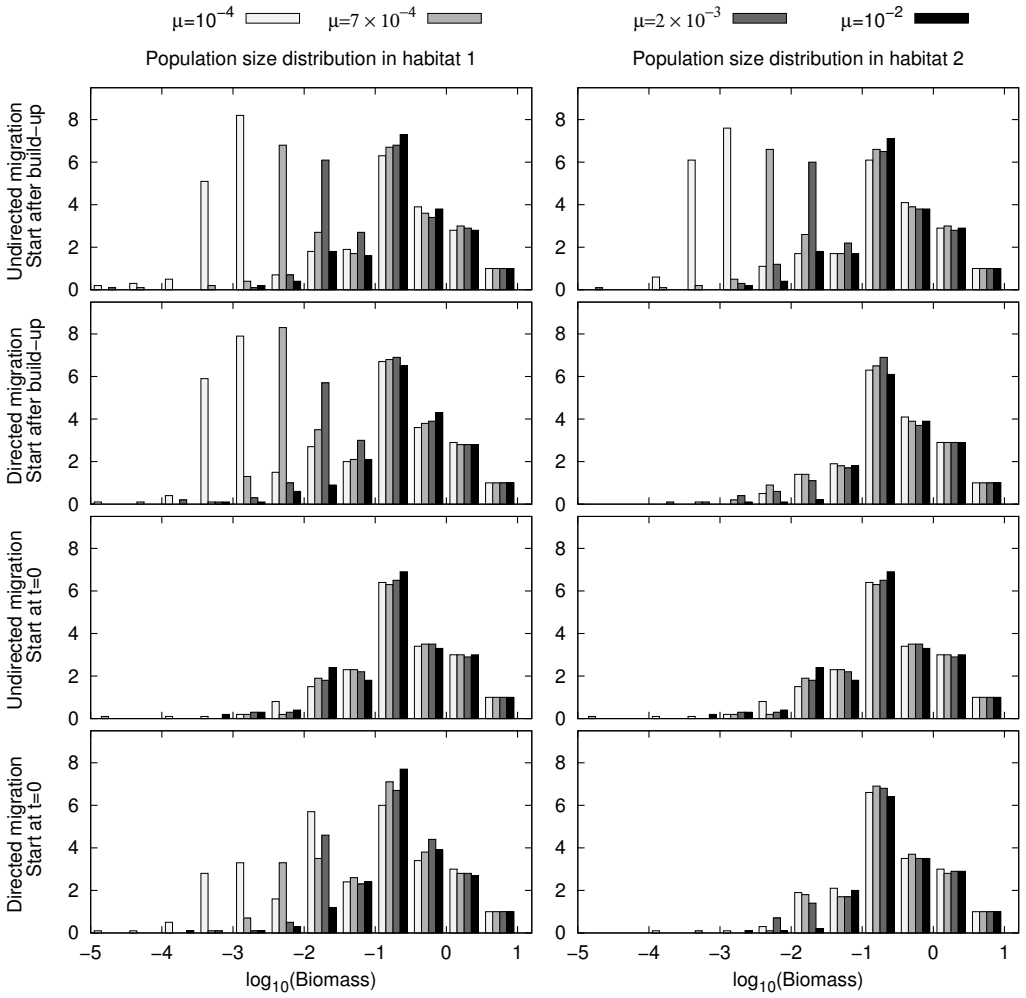

Figure 3.5.: Distributions of populations sizes for simulations of 4 different scenarios and for 4 values of the migration rate μ. Each column represents an average over 10 realizations with different random numbers. In all realizations, the resource had by far the biggest population ($N_0 \approx 8.8$). Isolated habitats show the same distribution as realizations with undirected migration starting at the beginning of the simulation (line 3).

populations. Note that this figure does not show the fact that all species are black or dark gray (see line 4 of fig. 3.2).

The number of species per habitat can be interpreted as the local diversity. In case of undirected migration, local and regional diversity are identical, since every species has populations on both habitats. In case of directed migration, the local diversities differ and the local diversity of habitat 1 is again the regional diversity. Hence, we observe that low migration rates can lead to an increased local diversity due to outcome 1, whereas high migration rates lead to a decreased regional diversity due to outcome 2.

The distribution of the species per trophic level reveals more details about the transition from small additional populations to the displacement of native species, as shown in fig. 3.4. Here, light gray represents small migration rates and dark gray represents high migration rates. Higher trophic levels show the transition at smaller values of the migration rate μ than lower trophic levels: In case of $\mu = 2 \cdot 10^{-3}$,

nearly no additional populations were observed on the fourth level, but many on the third and even more on the second level. This is probably due to the fact that in this model species on higher trophic levels have smaller populations than species on lower trophic levels, and therefore exert a lower competition pressure on the invaders. However, as also observed in fig. 3.3, the error bars are biggest for intermediate migration rates, indicating that dependent on the random numbers single simulations might deviate from this trend. This is due to the above mentioned fact that whole trophic levels (not only single species) show either outcome 1 or outcome 2, which leads to an increased number of possible network structures.

The population sizes of the invaders of outcome 1 depend on the migration strength, see fig. 3.5. In those scenarios that show the discussed transition between the outcomes and for low migration rates (light gray columns, $\mu = 10^{-4}$), we observe a bimodal frequency distribution of population sizes. In addition to the population sizes that also occur in outcome 2 for higher migrations rates (black columns, $\mu = 10^{-2}$), also peaks at smaller population sizes occur, which correspond to the additional populations of outcome 1. For higher migration rates, these peaks shrink and shift to larger populations sizes, in agreement with the smooth transition shown in the previous figures.

3.3 More complex variants

In order to get a deeper understanding of the system, we also performed more than 160 simulations of three scenarios, where either the spatial landscape or the migration is designed in a more complex way. In the following, some key results of these investigations are summarized. Eva Marie Weiel analyzed a system of two heterogeneous habitats (subsection 3.3.1) and a system with adaptive migration (subsection 3.3.3) [92]. Tobias Rogge extended the spatial scale in the context of his bachelor thesis and discussed migration on a chain of eight habitats (subsection 3.3.2) [93].

3.3.1 Inhomogeneous system

In real ecosystems, habitats can differ with respect to temperature, nutrients, resources, size, etc. To implement such inhomogeneous systems, Eva Marie Weiel performed simulations where the habitats differ either in their competition strength ($\alpha_{0,h=1} = 0.1$ and $\alpha_{0,h=2} = 0.02$) or in their competition range ($\beta_{h=1} = 0.25$ and $\beta_{h=2} = 0.125$) [92]. The migration in this variant is implemented as undirected diffusion as explained in subsection 3.2.1.

Both competition parameters have an important influence on the resulting network structures [1, 81]. Therefore, different network structures emerge in the two habitats if they are uncoupled (see upper line in fig. 3.6). Smaller values of the competition strength α_0 imply less intraspecific competition and therefore bigger,

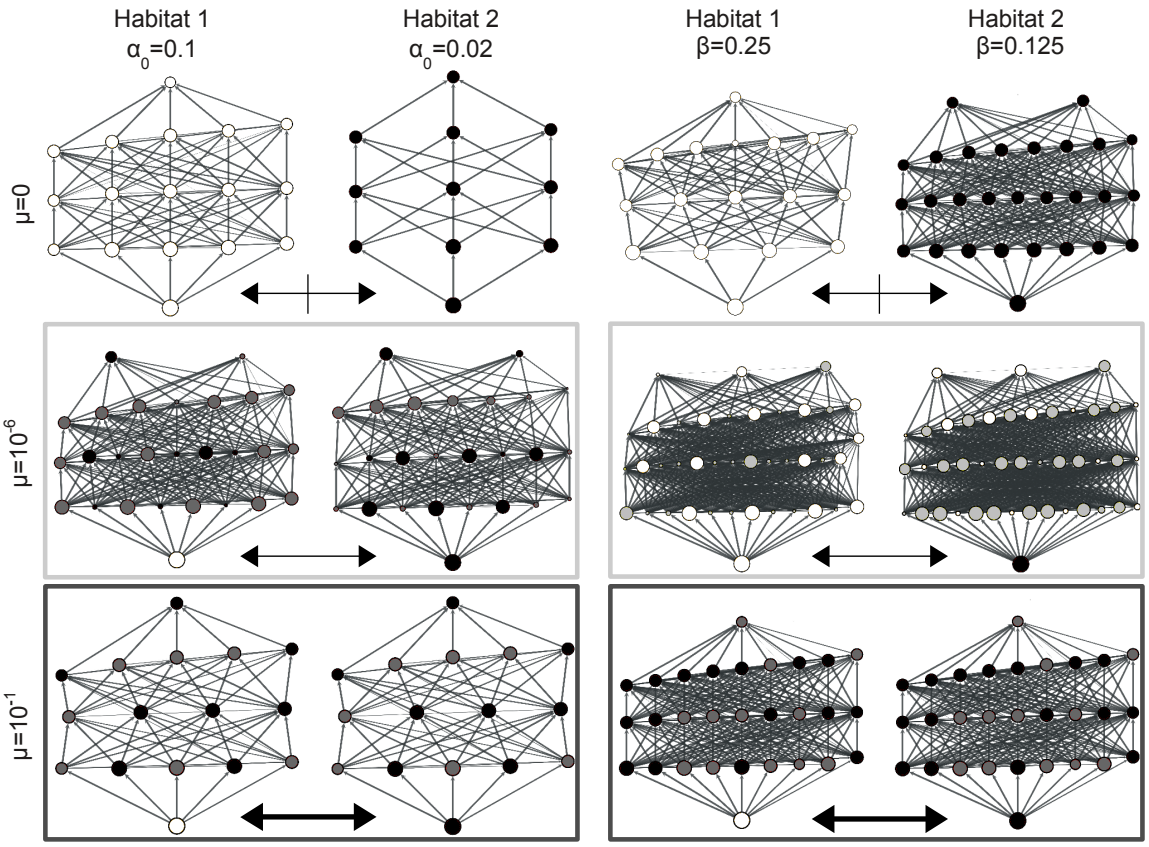

Figure 3.6.: Undirected diffusive migration between two habitats that differ in the competition strength α_0 (left) or in the competition range β (right). Migration is absent (top) or starts at $t = 0$ with $\mu = 10^{-6}$ (middle) or $\mu = 10^{-1}$ (bottom). For more explanations see caption of fig. 3.2. (Based on results from Eva Marie Weiel [92]).

but fewer populations because the energy provided by the resource can only support a certain total biomass (left). Smaller values of the competition range β imply less competitive exclusion, allowing for more species per trophic level (right).

When coupled by weak migration, the resulting networks look like a superposition of the isolated networks, see middle line in fig. 3.6. Each species exists in both habitats resulting in an increased number of populations. However, the population of one species is large in one habitat and small in the other, like the additional populations in outcome 1. Counting only the big populations, one recognizes the network structures of the isolated habitats. A stronger migration link (bottom line) leads to identical networks consistent with outcome 2. Similar network structures but with mixed colors can be obtained when migration starts after the networks have developed (not shown).

3.3.2 Chain of habitats

As a second variant with a more complex spatial landscape, Tobias Rogge analyzed a chain of 8 equivalent habitats [93]. Migration is again diffusive, with a constant

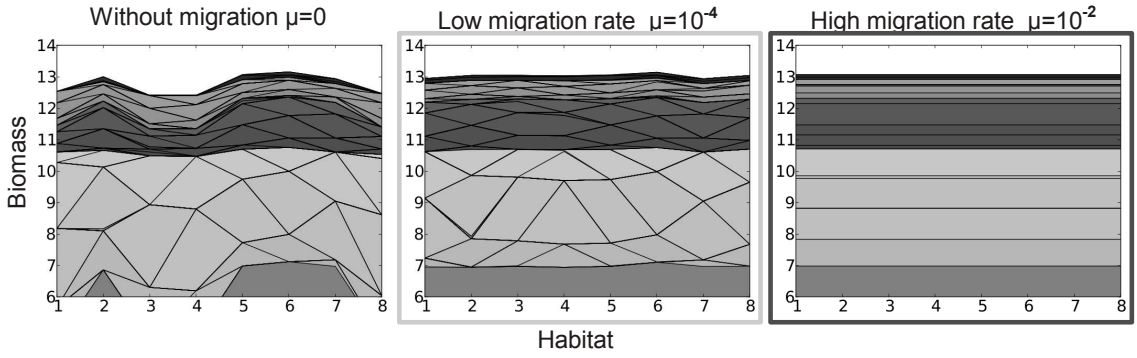

Figure 3.7.: Simulation outcome for undirected diffusive migration along a chain of 8 habitats. Migration starts after the initial build-up of the networks. Given is the biomass distribution of the resulting food webs before migration sets in (left panel) and after the emergence of new structures due to weak migration (middle panel) or strong migration (right panel). Networks of habitat 4 and 5 with weak migration are shown in fig. 3.8. (Based on results from Tobias Rogge [93]).

migration rate $\mu_{i,h\to h\pm1} = \frac{\mu}{2}$ between neighboring habitats $h \in [1,8]$. Hence, the additional migration term for species i on habitat h is

$$\ldots + \underbrace{\frac{\mu}{2}(N_{i,h+1} + N_{i,h-1})}_{\text{immigration}} - \underbrace{\mu N_{i,h}}_{\text{emigration}} \quad . \tag{3.2}$$

We choose closed boundary conditions, i. e. we set $N_{i,0} = N_{i,1}$ and $N_{i,9} = N_{i,8}$ in equation 3.2.

The increased number of habitats leads to a significantly increased program runtime. To keep it within a reasonable limit, the value of the feeding range is decreased to $s = 0.5$ (only for this variant). This leads to better adapted, but fewer predators and hence to a decreased system size of approximately $12 - 15$ species per isolated habitat.

In the left panel of fig. 3.7, the biomass distributions of eight isolated habitats are shown. Due to the randomly chosen mutant body masses, each network consists of a unique species composition. Some compositions seem to be more favorable than others in the sense that the total amount of biomass (of species and resources) is larger.

After all eight networks have fully emerged, migration is switched on. In the case of weak migration (middle panel) the situation is again similar to outcome 1, where the immigrating species can not establish themselves. Their populations stay much smaller than the natives and survive only due to the continuous migration into the habitat. These additional populations are too small to be visible in fig. 3.7, but are obvious in the example networks of habitat 4 and 5 shown in fig. 3.8. The color code in this figure is different to the previous figures. Black species with big populations in their native habitat 4 have small populations in their neighboring habitat 5 and vice versa. Also shown are small populations from the habitats further

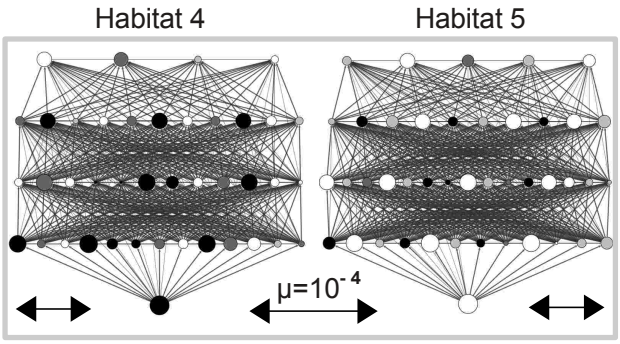

Figure 3.8.: Example networks on a chain of habitats weakly coupled by diffusive migration. The color code is different from the networks of fig. 3.2. Black (white) vertices: Species that originated in habitat 4 (5). Dark (light) gray vertices: Species that originated further on the left (right). (Based on results from Tobias Rogge [93]).

on the left in dark gray or further on the right in light gray. These additional populations have a major effect on the system concerning the biomass distributions. Even if the invaders can not establish themselves, they provide a continuous energy flow between the habitats. As a consequence, all biomass distributions equalize. This result does not depend on the recycling loop in equation (2.3), but occurs also when the recycling loop is switched off.

Stronger migration (right panel of fig. 3.7) leads again to outcome 2. Immigrating species can establish themselves and displace natives. Transiently very large networks occur while all species migrate in both directions and are present in many habitats at once. Then, by and by, the most favorable species composition (i.e., the one with the largest total biomass) displaces others and the resulting networks are identical. However, this process takes much longer than with only two habitats.

Tobias Rogge also discussed the same scenario of 8 habitats with a migration start at time $t = 0$ (not shown). Then, all networks co-evolve. If the mutation rate is still so small that a successfully mutant can spread over all habitats before a new mutant emerges, identical networks emerge, in consistency with the corresponding scenario of undirected diffusive migration between two habitats (line 3 in fig. 3.2).

3.3.3 Adaptive migration

Up to now, migration is diffusive and hence based on random movement. However, especially for higher developed species that can evaluate their current situation and possibly follow their prey or avoid competitors, this might be too simple. In this variant, we go back to 2 equivalent habitats, but instead of diffusive migration, two versions of adaptive migration are analyzed, where the migration rates of the species are dependent on their current growth rates $G_{i,h}$.

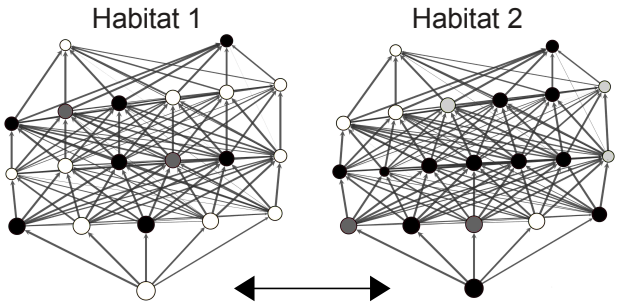

Figure 3.9.: Resulting networks of a simulation with undirected adaptive migration starting after the initial build-up at $t = 2 \cdot 10^6$. The migration rate of a species is proportional to the difference of its growth rates in the two habitats (Type 2), here with a factor $c = 10$. For more explanations see caption of fig. 3.2. (Based on results from Eva Marie Weiel [92]).

- Type I: A species i emigrates from habitat h if its population size in that habitat is currently decreasing,

$$\mu_{i,h\to h'} = \begin{cases} c \cdot G_{i,h} & \text{if } G_{i,h} < 0 \\ 0 & \text{else} \end{cases} \quad . \tag{3.3}$$

- Type II: Migration is directed into the habitat with better local conditions,

$$\mu_{i,h\to h'} = \begin{cases} c \cdot \left(G_{i,h'} - G_{i,h}\right) & \text{if } \left(G_{i,h'} - G_{i,h}\right) > 0 \\ 0 & \text{else} \end{cases} \quad . \tag{3.4}$$

Eva Marie Weiel varied the value of the proportionality factor c over three orders of magnitude from 10^{-2} to 10 [92].

With a migration start after the initial build-up of the networks, both types show in principle the same behavior. Since the system is most of the time near a fixed point with zero growth rate for all species, migration can only occur rarely, when the system is disturbed by a successful mutant. If the mutant replaces another species, this species has a negative growth rate and can hence migrate to the other habitat, where it can possibly replace an already existent species and establish itself. This can lead to completely different species compositions in the two habitats as shown in the example networks in fig. 3.9.

However, the general structure of the networks remains unchanged and is the same as that of isolated networks. The probability that a replaced species can successfully invade the other habitat increases with the proportionality factor c of the migration rate, in consistency with the previously discussed cases. With $c = 1$ only few species invade the other habitat successfully and with even smaller values of $c = 0.1$ or $c = 0.01$ the networks are basically isolated with very rare successful invasions.

The replacement of one species by a similar mutant or invader is a small perturbation of the whole system. Every prey or predator of the dying species experiences small fluctuations in its population size during the replacement. Consequently, other species can also migrate into the other habitat. However, additional mini-populations like in outcome 1 can not occur, since these disturbances and hence the migration rates are very small and occur transiently. Thus, these species cannot establish themselves in the other habitat and do not occur in fig. 3.9.

With a migration start at the beginning of the simulation, two mostly identical networks emerge (not shown). They differ at most by one single species, which just emerged in one habitat with a monotonously increasing population size and therefore did not have the opportunity to migrate. This is consistent with the corresponding scenario of diffusive migration between two habitats (line 3 in fig. 3.2).

3.4 Discussion

We have studied an evolutionary food web model on several habitats. Locally, species emerge, interact and go extinct according to the evolutionary food web model by Loeuille and Loreau [1]. Additionally, they migrate between habitats according to diffusive or adaptive dispersal. Migration may occur from the beginning, so that the food webs in the different habitats co-evolve, or it may occur later after the local food webs have become established.

Usually, our computer simulations show one of two frequent outcomes: Either the local food webs of the different habitats become mostly identical and have a similar structure and size as in an isolated system (outcome 2), or the local food webs differ with respect to the main species in each trophic layer, but include small populations from the neighboring habitats (outcome 1). These additional populations are sustained by ongoing immigration but cannot displace the native occupant of a niche. Generally, the food webs in the habitats show the regular structure that is characteristic of the model by Loeuille and Loreau [1]. They are clearly structured into distinct levels and each level consists of niches separated by a body mass difference that is equal to the competition range.

Which of the two outcomes occurs depends mainly on the migration rate and the time of migration onset. For intermediate migration rates, the two outcomes can combine, with part of the trophic levels being identical in the two patches, and with other levels being different and showing small populations from the other patch. Furthermore, we find that even for outcome 1 the total biomasses in the habitats become very similar to each other. To our knowledge, this result has not yet been observed in other studies. When the habitats are not equivalent because migration is directed or because the model parameters are different, the food webs can differ with respect to species number and population sizes. When migration occurs only under certain circumstances (for instance when the growth rate of a popula-

tion is negative), the species composition of neighboring habitats can become very different.

The model can not reproduce the sometimes catastrophic effect of species invasions into natural ecosystems, where alien species may find such good local conditions that their populations grow explosively leading to the extinction of prey or competitors species and a cascade of secondary extinctions [96, 97]. In the model by Loeuille and Loreau, species differ only with respect to body mass. If an invader or mutant successfully replaces a similar species, it has automatically the same predators and the same prey and hence the same function in the food web. Thus, the displacement of a species leaves the overall network structure unchanged. Once the initial build-up of the network is complete, all viable niches are occupied and stay occupied so that secondary extinctions can not occur. A different behavior with large extinction events and a more realistic species turnover will be observed in the new evolutionary food web model presented in chapter 4.

The complexity of real ecosystems exceeds by far the complexity of this model [98]. The interactions between species do not only depend on body mass, but also on many other species traits and also on environmental factors. The latter show considerable variations in space and time, causing species to change continuously, as for example implemented in a three patch metacommunity study presented by Loeuille and Leibold in 2008 [79]. After all, not only a changing environment, but also the local feedback between species and their environment makes the food webs and the migration behavior highly diverse [80].

The simple model studied in this chapter highlights those effects of migration on evolving ecosystems that already occur when only few traits are taken into account and when habitats are equivalent. The two main outcomes described above are widely observed in empirical and theoretical studies. Sax et al. [99] investigated invasions and extincts of land birds and vascular plants on oceanic islands. They found that for land birds the number of naturalizations of nonnative species is roughly equal to the number of extinctions, whereas for vascular plants species richness has increased by about a factor of two. The authors give several possible explanations for this behavior. One of them posits that nonnative species have become established because they are competitively superior to natives. If applied to birds, this would correspond to outcome 2. The increase in the number of plant species is similar to outcome 1. In our model, such an increase could be explained by ongoing immigration sustaining additional populations that would go extinct otherwise. However, this appears to be an unlikely explanation for oceanic islands, where the increased diversity is rather being attributed to an increased variety in local habitats, including those created by man [99].

Other theoretical studies of metacommunities also show the two types of outcomes. Mouquet and Loreau [66, 67] studied the effect of migration on local and regional diversity in a non-evolving metacommunity. Their model was later extended by Urban to contain adaptive phynotypic variation in the reproductive rates

of 20 competing species inhabiting 20 heterogeneous patches [73]. Without dispersal, all communities are unique and isolated, leading to a low local diversity and a high regional diversity. With a low or intermediate level of dispersal, regional diversity remains unchanged whereas local diversity increases due to immigration from neighboring communities. This corresponds to outcome 1, where the total number of species does not change after the onset of migration, but where the local number of species is approximately doubled (in a 2-patch system). Mouquet and Loreau predicted that higher levels of dispersal lead to homogenization of the metacommunity and hence to decreasing local and regional diversities, in consistency with our outcome 2.

Also many other studies suggest that local and regional diversity react differently to changes in the spatial landscape and dispersal [94]. Haegemann and Loreau [64] extended the investigations by analyzing different dispersal rates for resources and consumers leading also to local consumers with regional resources or regional consumers with local resources. The latter corresponds to our case of body-mass dependent migration rates, where species with small body masses in the lower trophic levels experience too small migration rates to successfully invade the other habitat, whereas the species compositions in the upper trophic levels are homogeneous. However, it should be mentioned that in the model by Loeuille and Loreau body mass differences are generally small and metabolic scaling of the migration rates has only weak effects.

Evolutionary species turnover is not necessary for all our results. In situations where migration is switched on only after the local food webs have become established, the two types of outcomes are also observed when the process of introducing new mutant species is stopped. However, in such a case no “gray” species would occur (see fig. 2), which are descendants of immigrants from the other habitat. Our computer simulations with adaptive migration, however, yield an outcome that could not be obtained in absence of evolution. Since migration rates are dependent on population growth rates, migration occurs only temporally, when the system is disturbed by the emergence of a new mutant. This leads to different species compositions in the two habitats. Just as the results of Loeuille and Leibold [78] mentioned in the introduction, these findings show that the interplay between space and evolutionary processes gives rise to new phenomena. However, we have to admit that the typical outcomes observed in our model do not appear to be very realistic. They can probably be attributed to the unusual stability of the model by Loeuille and Loreau. In general, adaptive behavior is known to have a considerable stabilizing effect on food web dynamics [26, 45], but it cannot become visible when dynamics is already very stable in the absence of adaptive behavior. Certainly, the study presented in this paper is only a modest beginning of the investigation of evolutionary food web models in space.

4 The new evolutionary food web model

The model presented in this chapter is introduced in the article "Evolutionary food web model based on body masses gives realistic networks with permanent species turnover", which was co-authored by Daniel Ritterskamp, Björn C. Rall, Barbara Drossel and Christian Guill. The article is currently under review [100].

The study is based on results from chapter 2, where I discuss what is generally needed in evolutionary food web models to generate diverse and complex networks. The model will be extended to several habitats in the following chapter.

I performed the simulations and wrote the main manuscript. However, all authors developed the model framework and made minor contributions to the final version of the article. The evaluation of the results in subsection 4.4.2 were done by myself and Christian Guill in close cooperation. The results of the model variants presented in subsection 4.5 were generated by Constantin Beck, Markus Schiffhauer and Janis Weigend in the course of their bachelor theses [101, 102, 103].

4.1 Introduction

In chapter 2 and 3 we have learned that the evolutionary food web model by Loeuille and Loreau [1] generates very regular networks that show an almost static behavior. The competition and feeding parameters define fixed viable niches, all of which are and remain occupied after the initial build-up. The idea of evolutionary food web models is to give insights into the conditions under which complex network structures can emerge and persist in face of ongoing species turnover, see subsection 1.2.3. In this context, a new model resulting in more complex and less static network structures is needed. The model presented here is based on the conclusion from chapter 2 that an evolutionary food web model has to fulfill two conditions to be able to generate diverse and complex networks.

First, it should allow for the evolution of few traits in addition to body mass in order to generate several possible survival strategies like for example specialists and omnivores. This idea is consistent with results from Rall et al. [28] and Eklöf et al. [90]. Second, the evolution of each trait has to be restricted in order to prevent unrealistic trends, for example towards extremely small or large body masses or towards extremely broad or narrow feeding ranges.

Our new model is less abstract than earlier models of this type (e.g. the web-world model [38, 39, 40, 41, 42] or the matching model [43, 44]) in the sense that all three evolving traits have a clear biological meaning. Similarly to the evolutionary niche model [45] and supported by empirical data regarding the body-mass ratios of predator-prey pairs [104, 105], we characterize a species by three traits with clear biological meaning: its own body mass (which determines its metabolic

rates), its preferred prey body mass, and the width of its potential prey body mass spectrum. The evolutionary rules in our model confine the traits within certain boundaries, without the requirement to include adaptive foraging.

The model most similar to our model is the one by Loeuille and Loreau [1]. It also uses the average adult body mass as a key trait and a similar concept for setting the feeding preferences. Our model differs from the model by Loeuille and Loreau in the number of evolving traits (3 instead of 1), the functional response (Beddington-deAngelis instead of linear), the competition rules (based on link overlap instead of body mass differences), the possibility of cannibalism and loops (included only in our model) and the resource dynamics. Moreover, we consider body mass ratios instead of body mass differences so that the body masses in our model spread over several orders of magnitude instead of only one. The bio-energetics of the species in our model follow well documented allometric scaling relationships [106], leading to networks with realistic body-mass scaling relations that can be tested directly against empirical data.

I demonstrate the capabilities of our model by evaluating 18 common food web properties and compare them to a data set of 51 empirical food webs from a large variety of different ecosystems. I further use the evolutionary model by Loeuille and Loreau [1] as a benchmark to assess the quality of the predictions of our model. In principle, both models are able to produce diverse networks. However, we obtain a higher variability in the feeding preferences and survival strategies and therefore more realistic values for the corresponding network properties. Moreover, while the network structures of Loeuille and Loreau are static, species turnover and extinction avalanches occur naturally in our model. This allows us to identify internal processes generating network structures that are prone to extinction avalanches. On this basis, we are able to discuss to what extent external factors are required for the occurrence of catastrophic extinction events.

4.2 Model description

The model includes fast ecological processes (population dynamics), which determine whether a species is viable in a given environment that is created by the other species, and slow evolutionary processes (speciation events), which add new species and enable the network to grow and produce a self-organized structure.

A species i is characterized by its body mass m_i, the center of its feeding range c_i, and the width of its feeding range s_i. These traits are subject to evolution. They determine the feeding interactions in the community (see Fig. 4.1) and thereby the population dynamics. A summary of all model parameters and variables is given in tab. 4.1. Note that the nomenclature differs from the model by Loeuille and Loreau presented in chapter 2 and 3.

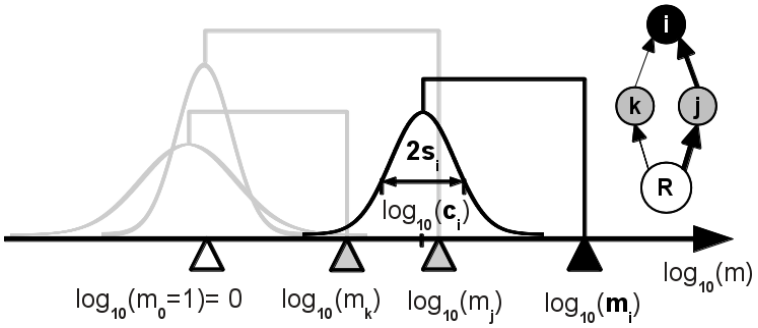

Figure 4.1.: Model illustration using 4 species. Species i (black triangle) is characterized by its body mass m_i, the center of its feeding range c_i, and the width of its feeding range s_i. The Gaussian function $N_{ij} = \exp(-(\log_{10} c_i - \log_{10} m_j)^2/(2s_i^2))/(s_i\sqrt{2\pi})$ (black curve) describes its attack rate kernel on potential prey species. Here, species i feeds on species j and k (gray triangles) with a high resp. low attack rate. Species k and j are consumers of the external resource, represented as species 0 with a body mass $m_0 = 1$ (white triangle). Also shown is the corresponding network graph.

4.2.1 Population dynamics

The population dynamics follows the multi-species generalization of the bioenergetics approach by Yodzis and Innes [107, 23]. The rates of change of the biomass densities B_i of the populations are given by

$$\dot{B_0} = G_0 B_0 - \sum_{j=consumers} g_{j0} B_j \tag{4.1}$$

for the external resource (species 0) and

$$\dot{B_i} = \sum_{j=resources} e_j g_{ij} B_i - \sum_{j=consumers} g_{ji} B_j - x_i B_i \tag{4.2}$$

for consumer species. $G_0 = R(1 - B_0/K)$ is the logistic growth rate of the external resource, e_j is the efficiency with which biomass of species j can be assimilated by its consumers, g_{ij} is the mass-specific rate with which species i consumes species j, and x_i is i's mass-specific respiration rate. The mass-specific consumption rate is given by

$$g_{ij} = \frac{1}{m_i} \frac{a_{ij} B_j}{1 + \sum_{k=res.} h_i a_{ik} B_k + \sum_{l=comp.} c_{il} B_l}, \tag{4.3}$$

where $a_{ij} = a_i \cdot N_{ij}$ is the rate of successful attacks of species i on individuals of species j, with the Gaussian feeding kernel N_{ij} given in Fig. 4.1. The parameter h_i is the handling time of species i for one unit of prey biomass, and c_{il} quantifies interference competition among predators i and l [108, 109, 13]. It depends on

parameter	meaning
resource	
$m_0 = 1$	body mass
$R = 1$	maximum mass-specific growth rate
$K = 100$	carrying capacity
B_0	biomass density
species i	
m_i	body mass
c_i	center of feeding range
s_i	standard deviation of feeding range
B_i	biomass density
population dynamics	
$e_j = 0.85/0.45$	assimilation efficiency for carnivores / herbivores
g_{ij}	functional response of predator i on prey j
a_{ij}	attack rate of predator i on prey j
$a_i = 1 \cdot m_i^{0.75}$	attack rate parameter
$h_i = 0.398 \cdot m_i^{-0.75}$	handling time of predator i
c_{il}	competition on species i from species l
c_{food}	competition parameter for food
c_{intra}	intraspecific competition parameter
$x_i = 0.314 \cdot m_i^{-0.25}$	respiration rate of species i
evolutionary rules	
$\omega = 10^{-4}$	mutation probability
$\epsilon = \frac{2}{10^4}$	extinction threshold

Table 4.1.: A summary of all model parameters. The values of the population parameters are based on [107]. If no value is given for a parameter, it is variable.

the similarity between species i and l, as measured by the overlap $I_{il} = \int N_{ij} \cdot N_{lj} d(\log_{10} m_j)$ of their feeding kernels, via

$$c_{il} = c_{food} \cdot \frac{I_{il}}{I_{ii}} \quad \text{for} \quad i \neq l. \tag{4.4}$$

The normalization of the competition with I_{ii} was proposed by Scheffer et al. [110] and accounts for the fact that the competition matrix is not symmetric. More specialized species exert a higher competition pressure than species with broad feeding ranges. The overlap I_{il} is similar to the niche overlap discussed by May [111].

The interference competition is assumed to be significantly higher within a species than between different species, e.g. due to territorial or mating behavior. To account for this, we introduce an intraspecific competition parameter c_{intra} and set $c_{ii} = c_{food} + c_{intra}$.

4.2.2 Speciation events

Each simulation starts with a single ancestor species with body mass $m_1 = 100$ and feeding parameters $c_1 = 1$ and $s_1 = 1$, which is thus feeding on the external resource with its maximum attack rate. The initial biomass densities are $B_0 = K = 100$ for the resource and $B_1 = m_1 \cdot \epsilon = 2 \cdot 10^{-2}$ for the ancestor species. The parameter ϵ is the extinction threshold and describes the minimum density required for a population to survive. At each unit time step, species below this extinction threshold get removed from the system.

A speciation event occurs with probability $\omega = 0.0001$ per unit time. This is so rare that the system is typically close to a fixed point before the next mutation occurs. Then, one of the currently existing species (but not the external resource) is chosen randomly as parent species i for a "mutant" species j. Thus, every species has the same probability ω/S to “mutate”, where S is the number of currently viable species. The logarithm of the mutant's body mass, $\log_{10}(m_j)$, is chosen randomly from the interval $[\log_{10}(0.5m_i), \log_{10}(2m_i)]$, meaning that the body masses of parent and mutant species differ at most by a factor of 2. The mutant's initial biomass density is set to $B_j = m_j \cdot \epsilon$ and is taken from the parent species. This implies that the parent species might go extinct if its biomass was close to its extinction threshold before the mutation event.

The mutant's feeding traits c_j and s_j are independent of the parent species. The logarithm of the feeding center, $\log_{10} c_j$, is drawn randomly from the interval $\left[\left(\log_{10}(m_j) - 3\right), \left(\log_{10}(m_j) - 0.5\right)\right]$, meaning that the preferred prey body mass is 3 to 1000 times smaller than the consumer's body mass. The width of the feeding range, s_j, is drawn randomly from the interval $[0.5, 1.5]$. A small value of s_j corresponds to a more specialized consumer, while a large value of s_j characterizes a consumer with a broad feeding range and lower attack rates. A combination of large preferred prey mass c_j and a wide feeding range enables a consumer to prey on species with a larger body mass than its own. This enables the emergence of cannibalism and feeding loops. The fixed intervals keep the evolving traits in reasonable ranges and prevent unrealistic trends, following the results from chapter 2.

4.3 Methods

The computer code for our simulations was written in C. I used the Runge-Kutta-Fehlberg algorithm provided by the GNU Scientific library [88] for the numerical integration of the differential equations. Simulations were run for $5 \cdot 10^8$ time units. For comparison, the generation time of the initial ancestor species with body mass $m_1 = 100$ is of the order of $\frac{1}{x_1} = \frac{100^{0.25}}{0.314} \approx 10$ time units.

The competition parameters c_{food} and c_{intra} have a strong effect on the diversity of the emerging food webs. To obtain the network variability observed in nature, I performed computer simulations with all four combinations of $c_{food} = 0.6$ or 0.8 and $c_{intra} = 1.4$ or 1.8. From each simulation run, I collected 80 food webs obtained after every $5 \cdot 10^6$ time units from $t = 10^8$ to $t = 5 \cdot 10^8$, resulting in a total of 320 different networks. Due to the initial build-up of the network, the first 10^8 time units were not taken into account.

The structure of the emerging food webs is compared to both empirical food webs and to food webs produced with the model by Loeuille and Loreau [1]. For the empirical data, we re-evaluated 51 of the 65 food webs from different ecosystem types analyzed by Riede et al. [112] for which we had body-mass data for all species in the network (see appendix for the complete list).

For the model by Loeuille and Loreau, we evaluated the final network structures obtained with 75 combinations of different parameter values. Due to the static network structure, I could not obtain different networks from one evolutionary simulation. The niche width was set to $nw = \frac{s^2}{d} = 0.5, 1.0, 1.5, 2.0, 2.5$ and the competition strength to $\alpha_0 = 0.1, 0.2, 0.3, 0.4, 0.5$, similar to the original work. To get networks of comparable size I decreased the competition range, $\beta = 0.025, 0.05, 0.075$.

Both models use Gaussian feeding kernels with in principle infinite width to describe the feeding interactions, meaning that each species can prey on every other species. Thus, for analysis, very weak links have to be cut off in order to obtain meaningful network structures. In our networks, we removed all links that contribute less than 75% of the average link to the total resources of a consumer. This criterion is weaker than it might seem, because most of the links of a predator are very weak and so is the average link strength. Our cutoff measure depends on both the attack rate and the prey's biomass density. It thereby mimics unavoidable sampling limits in empirical food-web studies. For the networks produced by the algorithm of Loeuille and Loreau we used the cutoff criterion of the original work and removed all links with an attack rate less than 15% of the respective predator's potential maximum attack rate, disregarding the prey's biomass density.

4.4 Results

To provide a basic understanding of the model behavior, I first discuss some typical simulation runs. The results of these simulations are subsequently compared to empirical data in subsection 4.4.2.

4.4.1 Typical simulations

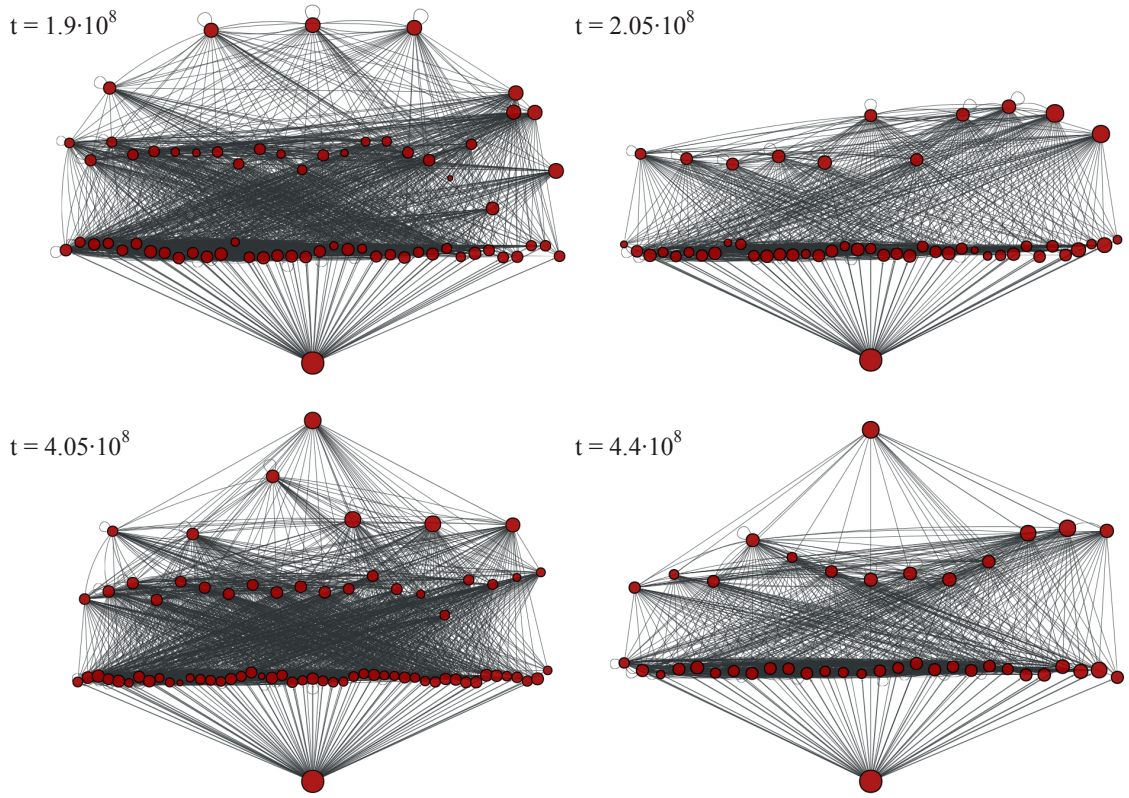

Figure 4.2.: Exemplary food webs for the time points indicated by vertical lines in fig. 4.3. The competition parameters were $c_{intra} = 1.4$ and $c_{food} = 0.8$.

A typical simulation run with the competition parameters $c_{intra} = 1.4$ and $c_{food} = 0.8$ is shown in fig. 4.3. Network visualizations for the time points indicated by vertical lines are shown in fig. 4.2. Each node represents a species, with the width scaling logarithmically with its biomass density. The vertical position of a species represents its flow-based trophic position, which is the average, weighted trophic position of its prey, plus one [12]. The arrows represent feeding links from a prey species to its predator species. Their width scales logarithmically with the biomass flow. It is obvious from the comparison of these network visualizations with the results in chapter 2 and 3 that the new evolutionary food web model produces more complex food webs than the model introduced by Loeuille and Loreau [1].

After an initial period of strong diversification, the system reaches a size of approximately 60 species (panel (a) in fig. 4.3) on 3 to 4 trophic levels above the

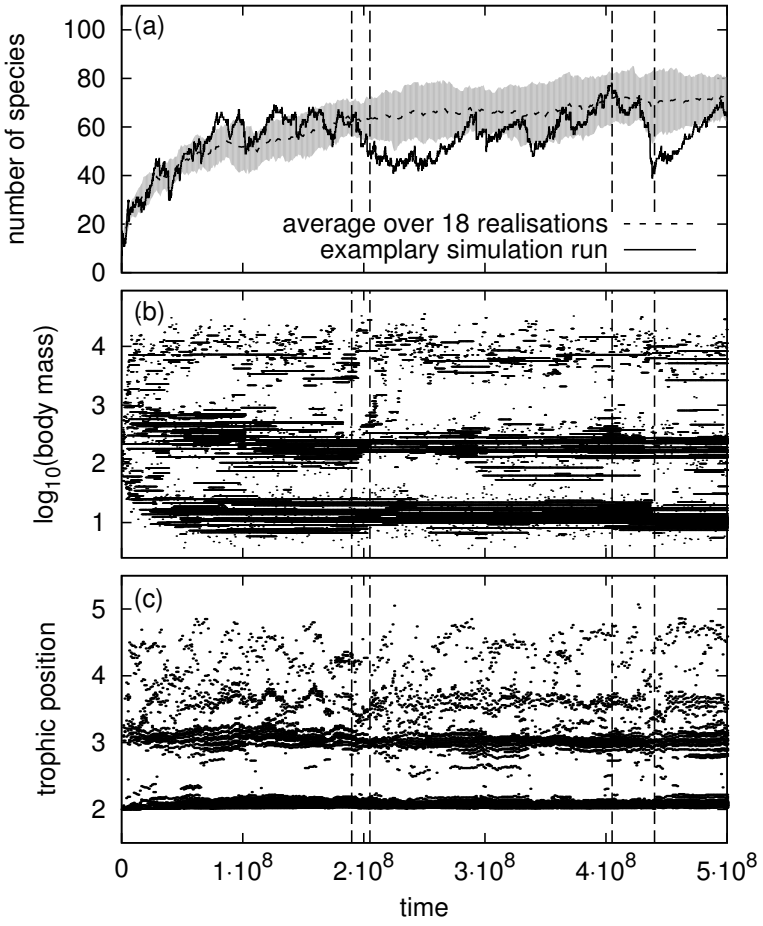

Figure 4.3.: Network size, body masses and flow-based trophic positions [12] of all species occurring during one exemplary simulation run with competition parameters $c_{intra} = 1.4$ and $c_{food} = 0.8$. Panel (a) also shows the average network size and its standard deviation for 18 simulations with identical parameters but different random numbers. Body masses and trophic positions were plotted at every 25th mutation event. Network visualizations for the time points indicated by vertical lines are shown in fig. 4.2.

resource (panel (c)). The species form clusters of similar body masses, as shown in panel (b). New predator and prey species emerge preferentially within these clusters: A prey species in a cluster experiences less predation pressure due to the saturation of the functional response of the predator, and the predation input of a predator is larger if its feeding preferences match such a cluster. Therefore, a trend towards strong specialization on these clusters occurs, resulting in the following network structure:

Species in the first cluster have a body mass of approximately 10^1, specialize on the resource and represent most of the second trophic level. Species in the second cluster with a body mass of approximately $10^2 - 10^3$ feed either on the resource (TL ≈ 2) or on the first cluster (TL ≈ 3). Species in the top cluster with a body mass greater than 10^3 specialize either on the first or on the second cluster and therefore

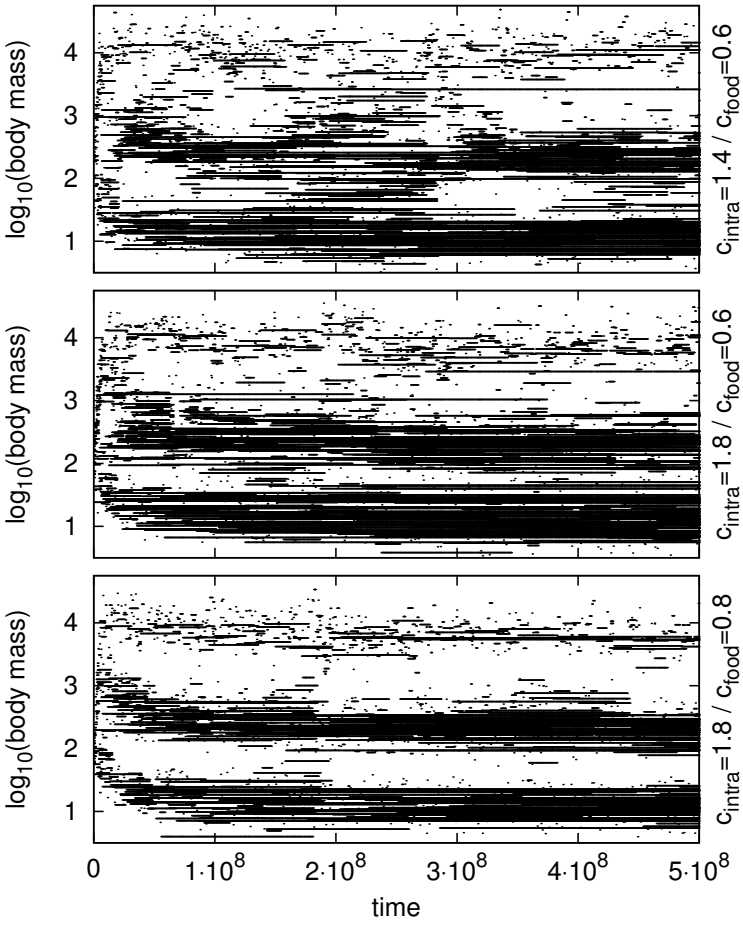

Figure 4.4.: Overview of the time series of three simulations with different values of the competition parameters.

have intermediate trophic positions ($3 \leq \mathrm{TL} \leq 4$). Some species have even higher trophic positions due to cannibalism and loops.

The initial build-up of the network continues until the species in the top cluster are close to the extinction threshold. Once all clusters have emerged, the system shows a continuous turnover of species. Mutants with very few predators can occur occasionally if their body mass is between two clusters and if the other species are specialized on the clusters. If such a mutant has viable feeding parameters, it can grow a large population and displace many other species at once, potentially even causing secondary extinctions. Examples for such extinction events are visible at $t \approx 2 \cdot 10^8$ and $t \approx 4.3 \cdot 10^8$. After an extinction event, the network rearranges, and temporally also species with broader feeding ranges appear, before the trend towards specialization followed by an extinction event starts again. A second driver of species turnover, in addition to this specialization-extinction-cycle, will be explained in chapter 5.

Both competition parameters c_{food} and c_{intra} have a strong effect on the diversity of the emerging food webs of our model. An overview of the time series of three other simulations is presented in fig. 4.4. Two trends can be observed: First, the

stronger the intraspecific competition c_{intra}, the smaller are the population sizes and the more populations can survive on the same amount of energy provided by the resource. Second, the stronger the competition for food c_{food}, the more often can species displace others resulting in rather small networks with fast evolutionary species turnover.

4.4.2 Network evaluation and comparison

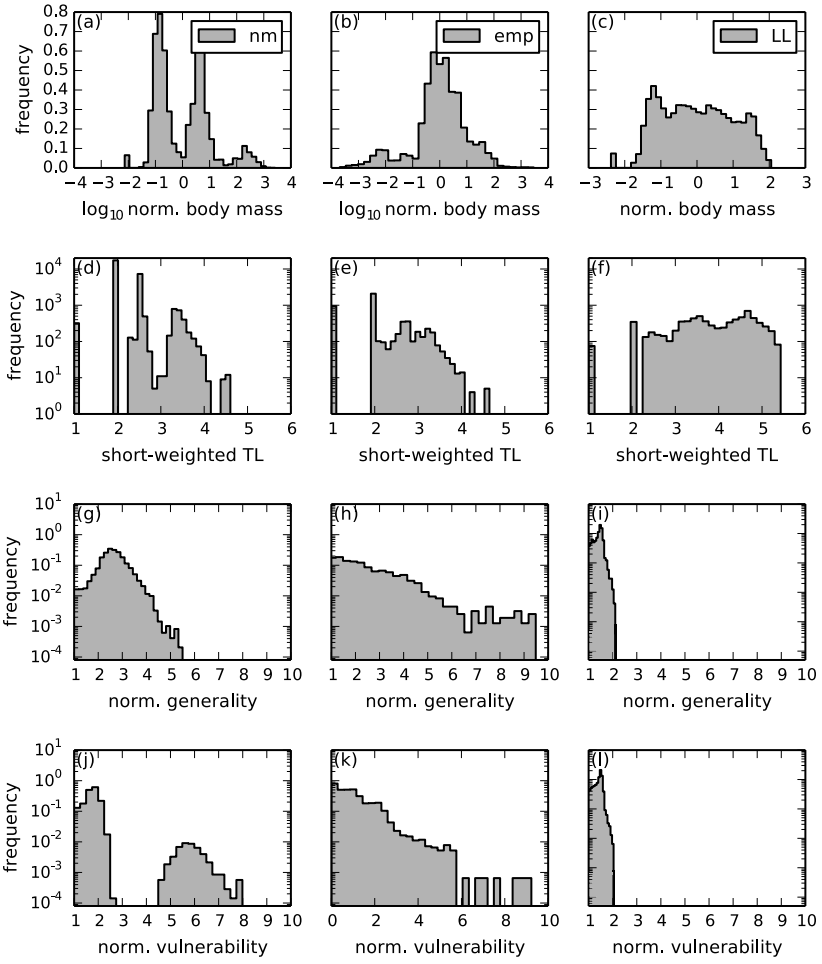

Figure 4.5.: Frequency distributions of body masses and short-weighted trophic level [12], as well as generality and vulnerability. The latter two are normalized by the number of links per species. **nm**: 320 networks from 4 simulations of our new model with all four combinations of $c_{food} = 0.6$ or 0.8 and $c_{intra} = 1.4$ or 1.8. **emp**: Average over 51 empirical food webs. **LL**: Average over 75 simulations of the model by Loeuille and Loreau [1]. Note that panel (c) shows absolute body masses, since in this model all body masses are in the same order of magnitude. See section 4.3 for more information.

We compared 320 networks from our model with 51 empirical networks and 75 networks from the model by Loeuille and Loreau [1], see fig. 4.5. Panels (a)-(c) show the distributions of body masses of all three data sets. The observed peaks in our simulated data correspond to the body mass clusters mentioned before. The

distance between the peak maxima is determined by the upper boundary of the mutation interval of the feeding center. Single empirical food webs show a similar peak pattern (not shown). In contrast, the body mass distribution of the model by Loeuille and Loreau looks blurred, due to our choice of the niche width $nw = \frac{s}{d}$. With smaller values of the feeding range s, the network structure is strongly layered and clusters of body masses that are multiples of the feeding distance d occur, where each species feeds on those in the cluster below and is prey to those in the cluster above [81].

Panels (d)-(f) show the distributions of trophic levels of all three data sets. Here, we use the short-weighted instead of the flow-based trophic level. This allows for better comparison with the empirical data for which the population sizes are often not available. The comparison between the two models reveals the main difference between the two different cutoff rules. A link with intermediate attack rate to a small prey population represents only a small proportion of the predator's diet. It is therefore neglected when using our cutoff threshold (75% of the average link). However, it is not recognized as a weak link with the cutoff rule by Loeuille and Loreau (15% of the maximum attack rate). On the other hand, a link with small attack rate to a big prey population (especially to the resource) is deleted in their model. Thus, trophic levels are overestimated, whereas our model with our cutoff rule results in a quite realistic distribution.

Both models have difficulties reproducing the empirical distributions of generality and vulnerability, which are much broader than the distributions produced by the models (panels (g)-(l)). For the model by Loeuille and Loreau, the distribution results from the fact that the species in the model feed only on prey with smaller body masses. The situation is similar to the cascade model [14], which also constrains predators to feed only on prey with a lower rank. Consequently, both generality and vulnerability cannot be larger than twice the average number of links per species. In our new model, the distribution of the vulnerability shows two humps. The first hump contains the carnivores in the higher trophic levels that feed on herbivores or on other carnivores. They have a high generality and a small vulnerability. The second hump contains the herbivores that feed on the resource. They are prey to many other species and hence have a high vulnerability.

We ascribe the differences between the models and the empirical distributions to the fact that both models have only one resource, which means that all herbivores feed on the same resource, whereas in empirical networks herbivores can have more than one resource. Furthermore, both models ignore the within-species body-mass distribution by assigning to each species a precise value of the body mass. This also narrows down the range of body masses a species can feed on or is vulnerable to.

number of species:	number of nodes in the network, S
links per species:	number of edges L divided by number of nodes S
connectance:	number of edges divided by maximum potential number of edges (S^2)
top:	number of top species (without a predator)
intermediate:	number of intermediate species (species with both predators and prey)
fraction omnivores:	fraction of species with prey from more than one trophic level
fraction herbivores:	fraction of species that feeds only on the external resource
generality:	distribution of number of prey species for all species, normalized with the average number of links per species
vulnerability:	distribution of number of predators for all species, normalized with the average number of links per species
linkedness:	distribution of number of prey species plus number of predators for all species, normalized with two times the average number of links per species
sd():	standard deviation of a distribution
mean trophic level:	mean of the short-weighted trophic levels of all species [12]
max. trophic level:	maximum over the short-weighted trophic levels of all species
fraction cannibals:	fraction of species with a cannibalistic link
fraction species in loops:	fraction of species that is part of at least one feeding loop, i.e., link patterns of the type i feeds on j j feeds on k, k feeds on i (excluding cannibalism)
chain number:	number of different food chains. To avoid divergence prior to calculating this number cannibalistic links are removed and feeding loops are cut open by removing links within loops where the predator is on a lower average trophic level than the prey.
clustering coefficient:	Probability that if species i and j are connected and j and k are connected, i and k are connected, too.
similarity:	defined for pairs of species i and j as number of links shared by the species divided by total number of links of the two species. We show the maximum over all pairwise similarities.
characteristic path length:	mean of average distance between any two species in the network (measured in feeding links)

Table 4.2.: The definitions of the 18 topological characteristics that are shown in fig. 4.6 and A.1.

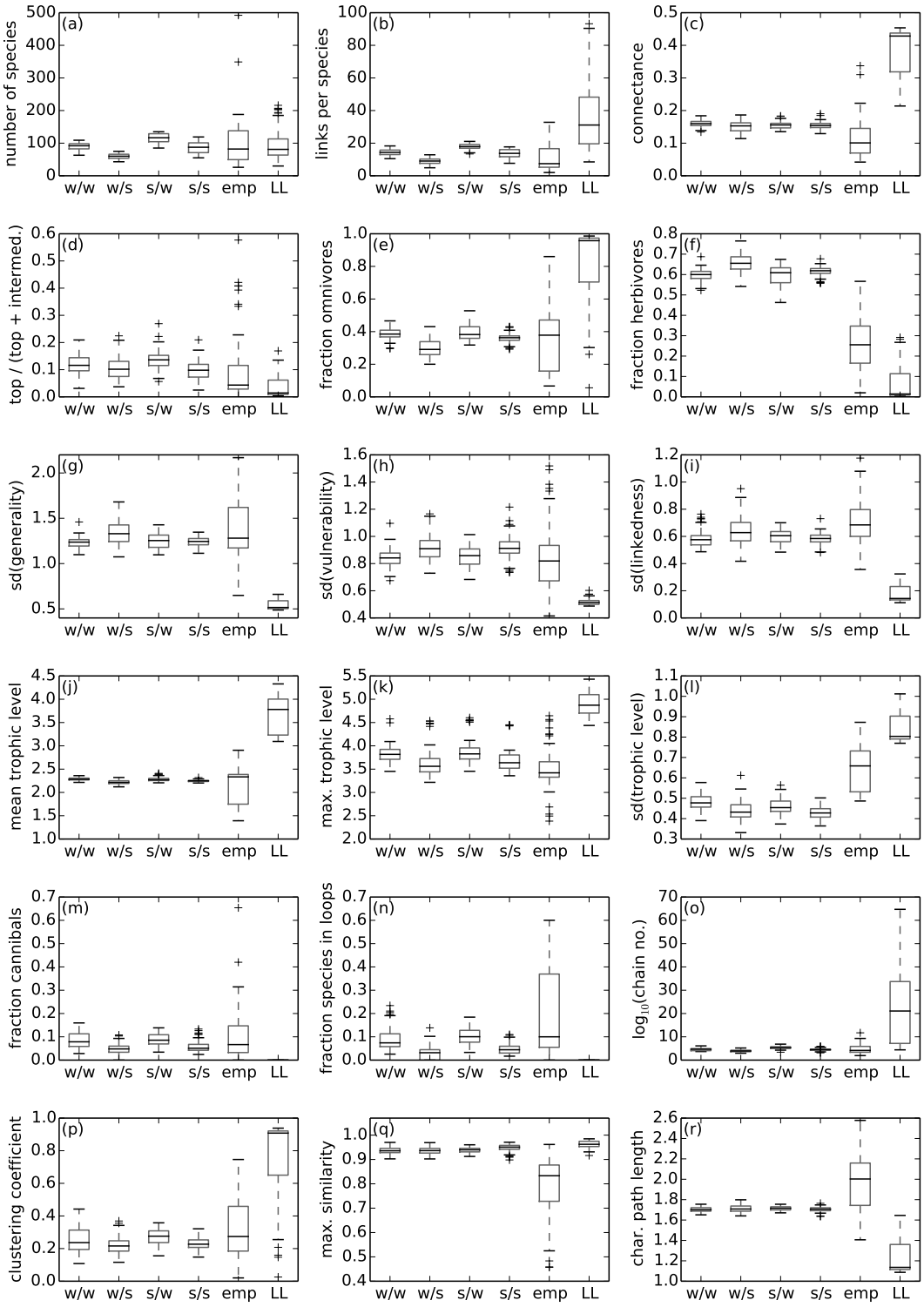

Figure 4.6.: Network properties of four realizations with different values of the competition parameters. **w/w**: Weak competition, $c_{intra} = 1.4$ / $c_{food} = 0.6$. **w/s**: Weak intraspecific competition and strong competition for food, $c_{intra} = 1.4$ / $c_{food} = 0.8$. **s/w**: Strong intraspecific competition and weak competition for food, $c_{intra} = 1.6$ / $c_{food} = 0.6$. **s/w**: Strong competition, $c_{intra} = 1.6$ / $c_{food} = 0.8$. **emp**: Average over 51 empirical food webs. **LL**: Average over 75 simulations of the model by Loeuille and Loreau [1]. See section 4.3 for more information. Details on the calculation of these network characteristics can be found in tab. 4.2

By analyzing the 320 networks from the 4 simulations separately (see panel (a) in fig. 4.6), we observe again the two trends concerning the competition parameters: First, the stronger the intraspecific competition c_{intra}, the smaller are the population sizes and the more populations can survive on the same amount of energy provided by the resource. Second, the stronger the competition for food c_{food}, the sooner can species displace others resulting in rather small networks with fast evolutionary species turnover. The definitions of the topological characteristics shown in the other panels are explained in tab. 4.2.

Both models are able to produce networks of realistic sizes, but tend to overestimate the number of links per species (panel (b)) and hence the connectance (panel (c)). The effect is much larger in the model by Loeuille and Loreau due to their original cutoff rule. This also explains the high fraction of omnivores and the low fraction of top and herbivorous species (panels (d)-(f)), as well as the high values of the number of chains and the clustering coefficient (panel (o) and (p)) and the small value of the characteristic path length (panel (r)). In fig. A.1 in the appendix, I demonstrate the effects of different cutoff levels. I also show how the networks generated with the model by Loeuille and Loreau [1] are affected when our cutoff criterion is applied.

Both models fail to reproduce the maximum similarity (panel (q) in fig. 4.6), due to the same reasons that also lead to the narrow distributions of generality and vulnerability. For the remaining panels, the model by Loeuille and Loreau performs worse than our model regardless which cutoff rule is used. For example, the short-weighted trophic levels (panel (j)-(l)) are not only overestimated due to the cutoff rule, but also reflect the regular network structure. As explained in chapter 2, these networks are layer-like structures, where each cluster represents one trophic level. Since all clusters accommodate a similar number of species instead of heaving more species on lower levels like in our model, the mean trophic level is overestimated. Moreover, the model does not include cannibalism (panel (m)) and loops (panel (n)), for which our model provides good predictions.

Due to the evolution of three instead of one trait, more diverse network structures emerge than with the model by Loeuille and Loreau. We observe a higher standard deviation of the generality, the vulnerability and the linkedness (panel (g)-(i)), reflecting different feeding preferences and survival strategies.

4.5 Model variants

I supervised three bachelor theses, which made a significant contribution to the understanding of the model behavior and helped to test the robustness of the model predictions with respect to the model details. Some key results of these investigations are briefly described in the following subsections.

4.5.1 Modified feeding interactions

One striking simplification of nature in the original model is that we describe a species by only three traits and that the existence of feeding links is determined only via the body masses of predator and prey species. Constantin Beck [101] introduced an additional model parameter p, which is the probability that a certain potential feeding link is really existent. For each feeding link with an attack rate α_{ij} of a predator i on its prey j, a random number $r \in [0,1]$ is called. The feeding link is regarded as existent, if $r < p$. Otherwise, α_{ij} is set to zero.

In this variant, two species with identical feeding parameters do not automatically share the same prey species. This mimics predators that differ in traits, which are not directly implemented in the model, like for example a reversed day and night rhythm or species living in different sub-habitats like treetop and undergrowth. In an extreme case, two species with identical feeding parameters can feed on two completely different sets of prey species. Therefore, the definition of the competition via the overlap of the attack rate kernels as explained in subsection 4.2.1 has to be modified. In order to calculate a meaningful competition term, this overlap is multiplied with the number of actually shared prey species and divided by the number of potentially shared prey species.

The bachelor thesis of Constantin Beck was developed, when the original model as presented above was still work in progress. After he finished his work, I introduced several minor changes to the model - for example the existence of cannibalism and loops. Therefore, his results are not quantitatively comparable to the results above. However, the qualitative behavior of the resulting networks with extinction waves and a continuous species turnover is the same.

The main effect of the link probability p is that the networks are in general smaller. This is due to a decreased competition: One prey less can result in a significantly reduced competition pressure. At the same time, it does not make a big difference for the feeding input of a predator, especially if the prey species is at the end of the predators feeding range in the tail of the Gaussian feeding kernel. Therefore, species are able to grow bigger populations, and the available resource supports fewer of these bigger populations.

The effect is observed for a broad range of p. Only in case of very small probabilities ($p < 0.3$), the networks get bigger compared to the original model. Then, the advantage of low competition values is overcompensated by very little feeding input, since every predator has only very few prey species. Hence, population sizes decrease and network size increases with decreasing link probability p. The lower the number of prey species, the more dependent are the predators on their prey, which makes them prone to secondary extinctions. Thus, networks get bigger, but less stable with decreasing link probability p.

4.5.2 Modified speciation rules

In the context of my studies on the model by Loeuille and Loreau, I learned that changing the evolutionary algorithm can have dramatic effects on the resulting networks, see section 2.3.2. The bachelor thesis of Markus Schiffhauer [102], together with the thesis of Jannis Weigend [103] presented in the following subsection, ensures that our findings are no artifacts of the specific choice of the evolutionary algorithm. Markus Schiffhauer discussed several variants of species dependent mutation rates.

1. Variant: The mutation probability is proportional to a species' biomass like in the model by Loeuille and Loreau [1].

2. Variant: The mutation probability is proportional to a species' inverse generation time and hence to $m_i^{-1/4}$ [113].

Markus Schiffhauer compared these two variants with the original model version, where each species has the same probability to mutate. The total biomass per trophic level decreases for higher trophic levels. However, on higher trophic levels are fewer species so that species with big body masses on high trophic levels have more biomass than smaller species on lower trophic levels. Therefore, the first variant favors species with big body masses to mutate. On the other hand, species with small body masses have shorter generation times and are therefore favored by the second variant.

These modifications influence the time dependency of the network development. For example, the recovery of the higher trophic levels after an extinction avalanche takes longer in the second variant, because mutations in these levels occur rarely. However, the changes in these two variants are rather small in the sense that each species still has a considerable probability to mutate so that each trophic level has a realistic chance to adapt to changes in the other levels. Thus, the overall network properties, like the total network size, the connectance, the distribution of body masses and the fraction of species or biomasses per trophic level, remain mostly unchanged. Also the trend towards strong specialization with subsequent extinctions as observed in the original model version occurs in these variants.

The situation changes in another variant:

3. Variant: The mutation probability is proportional to the number of individuals of a species.

In this case, species with big body masses have hardly any chance to mutate, because their individual density is decades smaller than the individual density of species with small body masses. Higher trophic levels hence do not occur (or take too long to be observed within a reasonable simulation time), which obviously alters the network structure. However, this variant seems to be unrealistic,

since it does not account for the fact that the establishment of a mutation is a stochastic process: Even if an individual with an advantageous mutation occurs, there is a certain probability that this individual won't have any descendants or that the descendants won't be carriers of this mutation. It can be shown, that this probability increases with increasing number of individuals [11].

4.5.3 Modified inheritance rules

In the third bachelor thesis by Jannis Weigend [103] different inheritance rules are analyzed. In the original model version, I use equally distributed random numbers in certain intervals to determine the traits of a mutant. Jannis Weigend changed this approach to normally distributed random numbers.

Concerning the evolution of the body masses m_i, the normal distribution is located around the parent's body mass and its standard deviation is varied between 0.09 and 1. With a cutoff at two standard deviations, this results in a maximum body mass factor between parent and daughter species between 1.5, describing local speciation events, and 100, describing species invasions from not explicitly modeled regions. The main effect is that species turnover becomes slower with stronger inheritance, because it is less likely that mutants with body masses between two clusters occur, which have few predators and cause extinction avalanches.

Concerning the evolution of the feeding traits, the normal distribution is located around the interval center used in the original model. Moreover, it is multiplied with a second normal distribution around the parent's trait. The first normal distribution keeps the feeding traits within reasonable boundaries (following the results of my first study [81]), whereas the second normal distribution introduces inheritance into the feeding parameters s_i and c_i.

If the parent species i and the mutant j have similar feeding centers, $c_i \approx c_j$, the initial build-up of different trophic levels and their recovery after an extinction avalanche is also slowed down. With very strong inheritance of the feeding center, all species will focus on the resource and no mutant emerges with a feeding center matching the first body mass cluster, leading to trivial structures with only one trophic level. If parent and mutant have a similar degree of specialization, $s_i \approx s_j$, all species exert and experience a similar competition pressure. Thus, instead of one species displacing another, both populations stay small and hence more populations per trophic level can survive and network size increases. However, small or intermediate degrees of inheritance in the feeding traits leave the network characteristics again mostly unchanged.

4.6 Discussion

In this chapter, I introduced a new evolutionary food web model where the feeding links are based on body mass, and where species differ by body mass, feeding center, and feeding range. By iterating population dynamics and speciation events for a sufficiently long time, complex food webs emerge, which show a high degree of commonality with empirical food webs. The new model is able to produce more realistic and more diverse network structures than the model by Loeuille and Loreau [1]. Species with similar body masses can have different feeding preferences and survival strategies, which is due to the larger number of evolving traits in our model. This leads to a higher variability in network characteristics such as linkedness, generality and vulnerability, even though natural variability is still larger, which is probably due to the fact that our model has only one basal resource and no body-size structure within species. In contrast to the model by Loeuille and Loreau, the new model allows for cannibalism and loops, since the feeding range can extend to body masses larger than that of the predator. An appropriate choice of the cutoff rule for weak links is essential for obtaining realistic results for connectance and trophic structure.

The increased number of evolving traits compared to the model by Loeuille and Loreau has also a large effect on the evolutionary trends and extinction events. The systems show an ongoing species turnover and are subject to constant restructuring. The species in our model form body mass clusters and the evolutionary process is characterized by a trend towards increased specialization on these clusters. Similar specialization trends have also been observed in other studies [45, 81]. The evolved predators gradually replace less efficient species with broader feeding ranges that cover also the gaps between the body mass clusters. We found that those broad ranged species have the role of keystone species that stabilize the networks against the occurrence of large extinction avalanches [114, 115]. In the absence of control by such predators, new mutants (or invaders) can find niches between two clusters with very little predation pressure, where they can grow to high abundance and cause extinction avalanches propagating from lower to higher trophic levels. After such extinction events, the empty niches can be reoccupied also by species with broader feeding ranges, before the speciation process starts again.

Our findings correspond to the results of Binzer et al [34], who identified specialized species on high trophic levels to be prone to secondary extinctions. Similar to our specialization mechanism, Mellard and Ballantyne [116] reported that coevolution of species does not necessarily lead to high levels of resilience for the ecosystem as a whole. A comparable turnover mechanism is missing in the model by Loeuille and Loreau. There, a displaced species is always replaced by a new species of a very similar body mass. And since the body mass is the only evolving trait, the new species has automatically the same predators and the same prey,

excluding the possibility of secondary extinctions or major changes in the network structure [81].

However, real ecosystems do show extinction events of different sizes, and their distribution evaluated over geological times resembles a power law [7]. For this reason, it has been suggested that ecosystems show self-organized criticality (SOC) [117], which means that the intrinsic dynamics of the systems is responsible for the power-law size distribution of extinctions. However, the question remains open due to sparse and ambiguous data [118, 11].

Some previous evolutionary food web models, for example the evolutionary niche model [45], exhibit SOC, whereas other models like the webworld model [39] or the model by Loeuille and Loreau [1] do not. The size distribution of extinction avalanches in our model is a power law with an exponent around 4 (not shown). Because of its steepness, this power law covers only approximately one decade, meaning that extinction events of more than 10 species are extremely rare. This is not the type of SOC required to explain the large extinction events in earth history, where up to 90 percent of all species went extinct. Regarding the time span a species is present in the system, our model is consistent with paleobiological data concerning the fact that higher trophic level species stay in the system for a much shorter time span than lower level species [118]. In view of the fact that large extinction events are ascribed to external drivers such as meteorite impacts and climate change, our model is consistent with the idea that the internal dynamics of ecosystems can drive smaller extinction avalanches, but not the large extinction events of earth history [118].

The evolutionary rules implemented in our model are very simplified and to some extend artificial. To make sure that our results do not depend on these simplified rules, we tested several variations concerning the mutation and inheritance rules. Our general finding is that minor changes in the evolutionary algorithm have only minor effects on the results. The overall mechanism with a trend towards specialization followed by an extinction event as explained above is robust to changes in the evolutionary rules. The time averaged network structures remain mostly unchanged. However, the typical time period for a specialization-extinction cycle may be influenced with extinction events being triggered sooner or later.

The fact that our networks show realistic patterns concerning many common food web properties suggests that our model provides a valuable tool to discuss urgent topics in ecological research. For example, the allometric equations are extendable by temperature terms (e.g. [119, 120, 121, 122, 123]). This approach would allow to model how warming might change evolution and extinction waves, in order to discuss current global change questions. A second idea would be to address habitat loss and habitat fragmentation as a prominent example of an external driver of extinction events [5, 6]. The findings from chapter 3 were associated with the applied competition rules and the remarkable stability of the model by Loeuille and Loreau, highlighting the assumption that a more realistic species turnover like in our new

model would probably lead to more realistic results and a better understanding of the interplay between evolving food web structure and spatial structure [91] . A third application was highlighted recently by Loreau, who emphasized the potential capabilities of evolutionary food web models (called "community evolution models" in his review) in the context of biodiversity and ecosystem functioning (BEF) [124]. The latter two ideas will be considered in the next chapter.

5 Evolutionary metacommunities II

Here, I present unpublished results of evolving metacommunities built with the evolutionary food web model presented in chapter 4. The spatial scenarios are very similar to the metacommunities built with the model by Loeuille and Loreau [1] discussed in chapter 3. The first part is about diffusive migration between two homogeneous habitats, see section 5.3. Subsequently, I discuss more complex scenarios in section 5.4. The results in subsection 5.4.2 were generated by Stephanie Kulpe and Theresa Hofman in the course of their bachelor theses [125, 126].

5.1 Introduction

In the previous chapter we have seen that the new evolutionary food web model is not only able to produce more realistic food web structures than the model by Loeuille and Loreau [1], but also results in food webs with an ongoing species turnover. This leads to a much broader range of phenomena in the time dependent behavior of the evolving food webs. Since this is already true for isolated habitats, the same can be expected even more so for coupled habitats.

The metacommunities analyzed here consist of two habitats that initially evolve separately. After a time span that is much longer than the typical time span of the initial build-up of the networks, both networks are coupled via a migration link. The networks then co-evolve together and are later de-coupled again. The migration link can be undirected or directed, the habitats can be homogeneous or inhomogeneous and the migration type can be diffusive or adaptive or density dependent. These scenarios mimic for example the coupling or decoupling of two waterbodies by the building or closing of a canal.

As in chapter 3, I focus on the influences of these spatial changes on the species composition, network size and network structure. Additionally, I extend my analysis and take up the idea of Loreau that evolutionary food web models provide an excellent tool to study the interplay of biodiversity and ecosystem functioning (BEF) [124]. The overall goals of BEF studies are to understand the mechanisms that mediate the functioning of diverse ecosystems and to predict the consequences of rapid changes in biodiversity [127]. Such changes in biodiversity can be triggered by changes in the spatial environment, e.g. by the opening and closing of dispersal routes as discussed here. In this context, metacommunity theory is tightly linked to the BEF debate. Appropriate measures that describe the functioning of ecosystems will be introduced in the following section.

During the last two decades, an enormous amount of BEF studies has been published that suggest many different theories, effects, hypothesis and mechanisms. Here, I confine myself to mention several review articles [128, 129]. Duffy et

al. introduced the concept of a horizontal diversity (within a trophic level) and a vertical diversity (across trophic levels) and grouped the mechanisms known so far within this framework [127]. Later, also Cardinale et al. [130] gave a good overview of five early hypothesis about multi-trophic BEF. Both reviews point out that most BEF studies so far focus on rather simple systems (for example only one trophic level) on rather small spatial and temporal scales. Therefore no clear picture of the interplay of biodiversity and ecosystem functioning in real ecosystems exists so far.

An example of a theoretical study with many species on several trophic levels is the study of Schneider et al [131]. The authors reject a long-established hypothesis, which suggests the release of the basal community from feeding pressure with growing functional diversity, due to an increased intraguild predation within the consumer community [127, 132, 133]. Schneider et al. showed that such an increase of the functional diversity indeed leads to an increased intraguild predation in the consumer community, but not to a decrease of the total biomass of the basal community. A diverse predator community might hence be less efficient than a species-poor community but, at the same time, more exploitative.

However, Schneider et al. did not take any spatial influences into account, although ecosystems are obviously not closed, but experience spatial exchanges of energy and matter [127, 46]. Moreover, they investigate network structures with species compositions that were generated with a stochastic algorithm. These food webs are analyzed on very small temporal scales without any species turnover. The same is true for many other studies that either also assume static network structures or that apply random extinction events without the emergence of new species instead of realistic turnover algorithms [127, 130].

With our new evolutionary model, it is possible to investigate the time dependent behavior of the functioning of large food webs. The species are not randomly put together, like for example done by Schneider et al [131], but emerge via coevolution leading to more realistic and dynamic network structures. My results of isolated habitats support the observation of Schneider et al. that an increase in the predator diversity does not release the basal community from feeding pressure.

My results of coupled habitats reveal a spatial rescue effect, which influences the network evolution. The resulting network structures are thus strongly dependent on the current spatial situation. Thus, in addition to short-term responses of ecosystems to changes in their spatial environment, also long-term recovery and adaptation to the new situation afterwards can be investigated. A similar interplay between evolutionary and spatial aspects does not occur with the model by Loeuille and Loreau. Moreover, it is naturally excluded in previous (typically non-evolving) metacommunity and (typically non-spatial and non-evolving) BEF studies. However, it does exist in nature [71]. Metacommunities built with our new evolutionary model therefore provide a promising new perspective to metacommunity theory and to the BEF debate.

5.2 Measures of ecosystem functioning

In the simulations presented in the following subsections, six measures of ecosystem functioning will be evaluated. I analyze their temporal behavior during the initial build-up of the isolated networks and how they are influenced during the migration interval. The calculation of these measures is derived from the work of Schneider et al. [131].

1. *The functional diversity FD:*
   A new diversity measure needs to be introduced. The diversity measured as the pure number of species does in fact have only a limited explanatory power about how "diverse" a community is. For example, two species with similar traits usually have a similar position and hence function in the food web. Those species are called redundant, because when one of these species goes extinct, the other one might still be able to retain their function in the network. Hence, large extinction events may change the diversity, but leave the functional diversity unchanged.

   Here, I calculate the envelope of all Gaussian feeding kernels N_{ij} (see fig. 4.1) of all species. The functional diversity is regarded as the integral of this envelope over the whole body mass axis,

   $$FD = \int_{-\infty}^{+\infty} ENV_i\left(N_{ij}\right) d\left(log_{10}(m_j)\right). \tag{5.1}$$

   The species in the model are typically specialized on body mass clusters, as explained in subsection 4.4.1. All species feeding on the same body mass cluster have similar feeding traits. Thus, since the integral over one single feeding kernel is normalized to 1, the functional diversity roughly corresponds to the number of body mass clusters.

2. *The total biomass density of consumer species C:*
   Up to now, we have observed several times that smaller population sizes correspond to larger network sizes. This suggests that the total amount of biomass of all species might be rather insensitive to the restructurations in the network. In order to test this hypothesis, I simply add up all biomass densities of all species,

   $$C = \sum_{i=1}^{S} B_i. \tag{5.2}$$

3. *The total biomass density of resources species R:*
   This measure does not have to be calculated. Since we have only one single resource in this model, it is simply $R = B_0$.

4. *The total energetic loss due to metabolism of consumers X_C:*
   To calculate this measure, I add up the metabolic losses of all consumer species,

$$X_C = \sum_{i=1}^{S} x_i \cdot B_i, \tag{5.3}$$

   where $x_i \cdot B_i$ is the energetic loss of species i, as in eq. 4.2. Schneider et al analyzed an equivalent measure for their resources as well. Here, we have only one resource that grows logistically, which makes such a measure unnecessary.

5. *The total consumption rate on basal species F_{CR}:*
   This corresponds to the total amount of biomass flow per unit time from the resource to the consumer species in the network. Note, that the appropriate value of the herbivorous efficiency $\epsilon_0 = 0.45$ has to be used,

$$F_{CR} = \sum_{i=1}^{S} \epsilon_0 \, g_{i0} B_i. \tag{5.4}$$

   The sum is over all species, where g_{i0} is the consumption rate of species i on the resource, as in eq. 4.2.

6. *The intraguild consumption rate F_{igp}:*
   This corresponds to the total amount of biomass flow per unit time within the network. Schneider et al. called this measure intraguild predation. Note, that the appropriate value of the carnivorous efficiency $\epsilon_j = 0.85$ has to be used,

$$F_{igp} = \sum_{i=1}^{S} \left(\sum_{j=1}^{S} \epsilon_j \, g_{ij} B_i \right). \tag{5.5}$$

   The sum is again over all species, where g_{ij} is the consumption rate of species i on species j, as in equation 4.2.

5.3 Diffusive dispersal between two homogeneous habitats

This section contains results from simulations that were performed analogously to the simulations in section 3.2 with the model by Loeuille and Loreau [1]. The setting describes dispersal in a metacommunity of two habitats that are coupled by an undirected (subsection 5.3.2) or directed (subsection 5.3.3) migration link.

5.3.1 Modeling dispersal

As in section 3.2, I model dispersal as diffusive migration between two habitats. Therefore, the differential equation 4.2 is extended by two extra terms describing the biomass loss and gain of species i due to emigration and immigration.

$$\ldots - \underbrace{\mu_{i,h\to h'} N_{i,h}}_{\text{migration from } h \text{ to } h'} + \underbrace{\mu_{i,h'\to h} N_{i,h'}}_{\text{migration from } h' \text{ to } h} \qquad \left[h, h' \in [1,2],\ h \neq h'\right] \tag{5.6}$$

The migration rate scales allometrically, $\mu_{i,h\to h'} = \mu_{h\to h'} \cdot m_i^{0.25}$, where species with bigger body masses are able to migrate faster. In this model, taking allometric scaling into account does make a difference, because the body masses of the species span over several orders of magnitude, in contrast to the model by Loeuille and Loreau [1].

Migration can be either undirected ($\mu_{1\to 2} = \mu_{2\to 1} = \mu$) or directed from habitat 2 to habitat 1 ($\mu_{1\to 2} = 0$ and $\mu_{2\to 1} = \mu$). The migration link is switched on after $5 \cdot 10^8$ time steps and switched off after $1.5 \cdot 10^9$ time steps. I varied μ over several orders of magnitude, $\mu \in \left(10^{-1}, 10^{-2}, \ldots, 10^{-6}\right)$ and performed several realizations for each value and each spatial scenario.

The extinction criterion is applied only before the next mutation event takes place, with the same argument as in section 3.2.1. This protects mutants that emerge locally, and whose biomass can initially fall below the extinction threshold before the establishment in both habitats. In order to simplify the evaluation, mutation events take place at every 10^4-th time step. Then, first the mutation habitat and afterwards the parent species is chosen randomly.

The coupling of two habitats and hence the increased number of species in the system leads to a significantly increased program runtime. To keep it within a reasonable limit, I vary the values of the feeding parameters to $c_{food} = 1.0$ and $c_{intra} = 0.25$. This leads to a decreased system size of approximately 15 species per isolated habitat but does not influence the overall behavior of the model.

5.3.2 Undirected migration

A typical simulation run is shown in fig. 5.1. Initially, the two habitats evolve separately. The biomasses of the resources slightly decrease as long as the networks are still growing. This is consistent with the observation of Schneider et al [131] and rejects long-established hypotheses about trophic cascades [127, 132, 133]. The other measures of ecosystem functioning approach some value and fluctuate around it, which reflects the ongoing restructurations due to species turnover.

Migration sets in after $t = 5 \cdot 10^8$ time steps. Similar to outcome 2 in section 3.2, undirected migration leads to identical networks. The local diversity (=number of

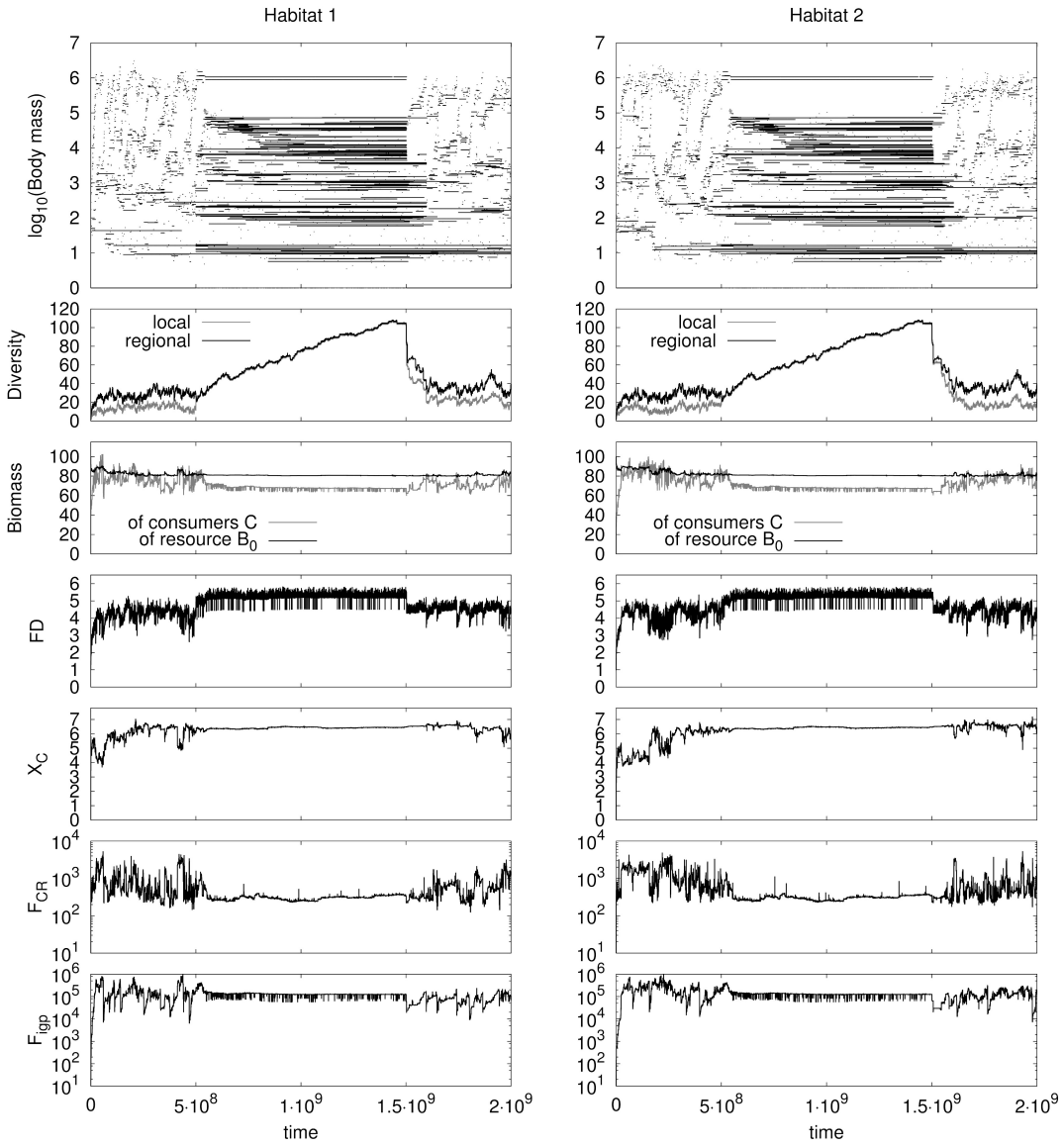

Figure 5.1.: An evolutionary metacommunity of two habitats coupled via an undirected migration link. The migration rate is $\mu = 10^{-5}$ in the time interval $5 \cdot 10^8 < t < 1.5 \cdot 10^9$ and zero otherwise.

species present in one habitat) becomes identical to the regional diversity (=total number of species in the system), since each species now has a population on each habitat. The regional diversity initially slightly decreases when native species are displaced by immigrants. The resulting networks right after the onset of migration contain a mixture of species from both habitats. Apart from that, the network structure is the same as of isolated networks.

Without evolution, the networks would simply stay in this situation and persist over time. However, due to the interplay of evolution and dispersal, a new behavior emerges. The two coupled networks behave differently than two isolated habitats. This can be explained with a spatial rescue effect that exists as long as migration is switched on.

Whenever a mutation event takes place, the mutants initial biomass density is taken from the parent species. If the parent species has a big body mass, it is typically very close to its own extinction threshold, which means that the mutation either can not take place at all or that the parent species does not survive it. Thus, if the mutation takes place and if the mutant is viable, it does not have to compete with its parent species. And if the mutant is not viable, both of them are removed from the system mimicking evolutionary suicide [32]. This seems to be a second driver for the species turnover in this model, in addition to the specialization-extinction-process discussed in the previous chapter.

This mechanism can be destroyed in a metacommunity. Then, the parent species is only locally extinct. If the mutant is not viable, the parent species simply reoccupies the mutation habitat via immigration from the other habitat and the situation is the same as before the mutation. Evolutionary suicide is now excluded. A mutant that would be viable in an isolated habitat in the absence of its parent species, has to overcompensate the competition with its parent species in addition to its own emigration losses in the metacommunity. The probability for a mutant with big body masses to become established and to replace its parent species is reduced. As a consequence, the species turnover in the higher trophic levels is dramatically slowed down.

This spatial rescue effect for the parent species thus stabilizes the higher trophic levels and subsequently has a major impact on the whole network. It seems as if in the isolated habitat viable niches occur and vanish faster than they can be completely occupied. In a metacommunity, the persistent top predators define persistent niches and evolution leads to a complete filling of these niches. This explains the increase of the diversity in the system.

The long-term behavior of the coupled system is not obvious from the simulations performed so far. The simulation runtime is too short to predict whether the diversity saturates at some point or whether large extinction events still occur or whether an evolutionary stable state can be reached. In fig. 5.1, it seems as if the diversity immediately decreases, as soon as the migration is switched off. This is misleading. In fact, both networks are able to persist without any changes even without the coupling. The collapse is triggered by mutation events soon after the decoupling, when the evolutionary suicide is again possible.

Even if the networks experience dramatic changes in their diversity, the six measures of ecosystem functioning analyzed here hardly change - except for showing less fluctuations when migration is switched on. For example, the total energetic loss of consumers X_C, the total consumption rate on basal species F_{CR} and the intraguild predation F_{igp} stabilize at some intermediate value during the coupling due to the overall stabilizing influence of the rescue effect.

A principle that has been mentioned several times during this work is that more species per trophic level correspond to smaller population sizes. This can now be expressed via the measures of ecosystem functioning: the total biomass of the

consumer species C is even slightly smaller than in isolated habitats. Thus, the increased number of species still exert a similar predation pressure on the resource leading to a resource biomass B_0 that does not significantly change due to the migration link.

We observe that the dramatic change in diversity due to the rescue effect does not lead to a dramatic change in the functional diversity. During the migration interval, body mass clusters persist over time. The addition of redundant species does not lead to new clusters but simply to more species per cluster, which hardly affects the functional diversity. It increases only slightly during the filling of all viable niches after the onset of migration and stays constant afterwards. The downwards peaks correspond to situations where a species with big body mass becomes locally extinct due to a mutation process and subsequently re-immigrates from the other habitat.

All effects of the migration link described in this subsection can be observed for a wide range of migration rates. I varied the value of the migration rate μ between 10^{-1} and 10^{-6} and found no indication for a dependency on the migration rate μ. It simply influences the time span the system needs to reach the next equilibrium after a mutation event. In the simulation presented in fig 5.1, this time span is typically much smaller than 10^4, which is the time span between two mutation events. Thus, migration acts on a similar timescale like population dynamics and is much faster than the evolutionary processes. Other results can be expected in case of much smaller migration rates or in case of other spatial topologies, as shown in the following subsections.

5.3.3 Directed migration

In contrast to the results of undirected migration, the results of directed migration are very sensitive to the exact value of the migration rate μ. Dramatic changes appear in case of a high migration rate (fig. 5.2) and minor changes appear for smaller migration rates (fig. 5.3). Moreover, both habitats experience different changes since the migration is now asymmetric.

Habitat 2 looses biomass due to emigration. Species in high trophic levels have to overcompensate their own migration losses in addition to shrinking prey populations. Therefore, high trophic levels collapse, as shown in fig. 5.2. This is consistent with the results of chapter 3.2.2 (see second line in fig. 3.2). However, in contrast to the results with the model by Loeuille and Loreau, the network adapts to this new situation and a new structure emerges after the coupling. The remaining species experience less predation pressure due to the loss of predators. Additionally, they reduce their population sizes due to their own emigration losses. The reduction of population sizes plus the decreased predation pressure enables new species to emerge within the same range of body masses. Thus, the number of species recovers and eventually even exceeds the previous network size.

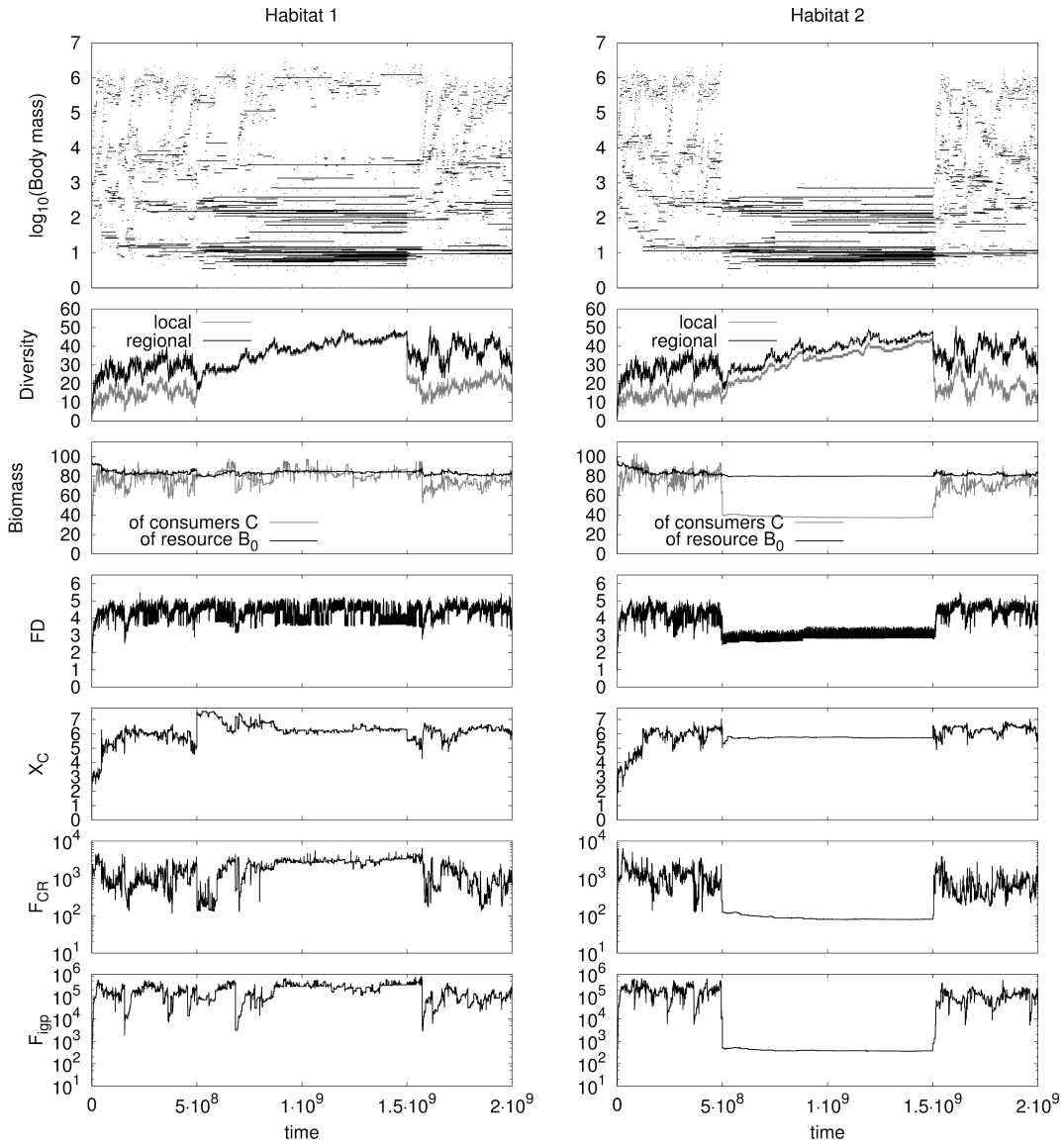

Figure 5.2.: An evolutionary metacommunity of two homogeneous habitats coupled via a strong, directed migration link from habitat 2 to habitat 1. The migration rate is $\mu = 10^{-2}$ in the time interval $5 \cdot 10^8 < t < 1.5 \cdot 10^9$ and zero otherwise.

The functional diversity FD decreases and the intraguild predation F_{igp} is reduced by several orders of magnitude, reflecting the new network structure of only one single trophic level above the resource. The total energetic loss X_C and the total consumption rate on the resource F_{CR} decrease as well, reflecting the decreased population sizes and the therefore decreased predation pressure on the resource. As soon as migration is switched off, higher level species can again emerge and the network quickly recovers to its former structure. The described emigration effect becomes weaker for lower values of the migration rate μ. In case of $\mu = 10^{-5}$, see fig. 5.3, the emigration loss is so small that no obvious changes in the network structure of habitat 2 occur.

The food web structure in the immigration habitat 1 is also influenced by the coupling. Initially, many native species are displaced by immigrants and the regional

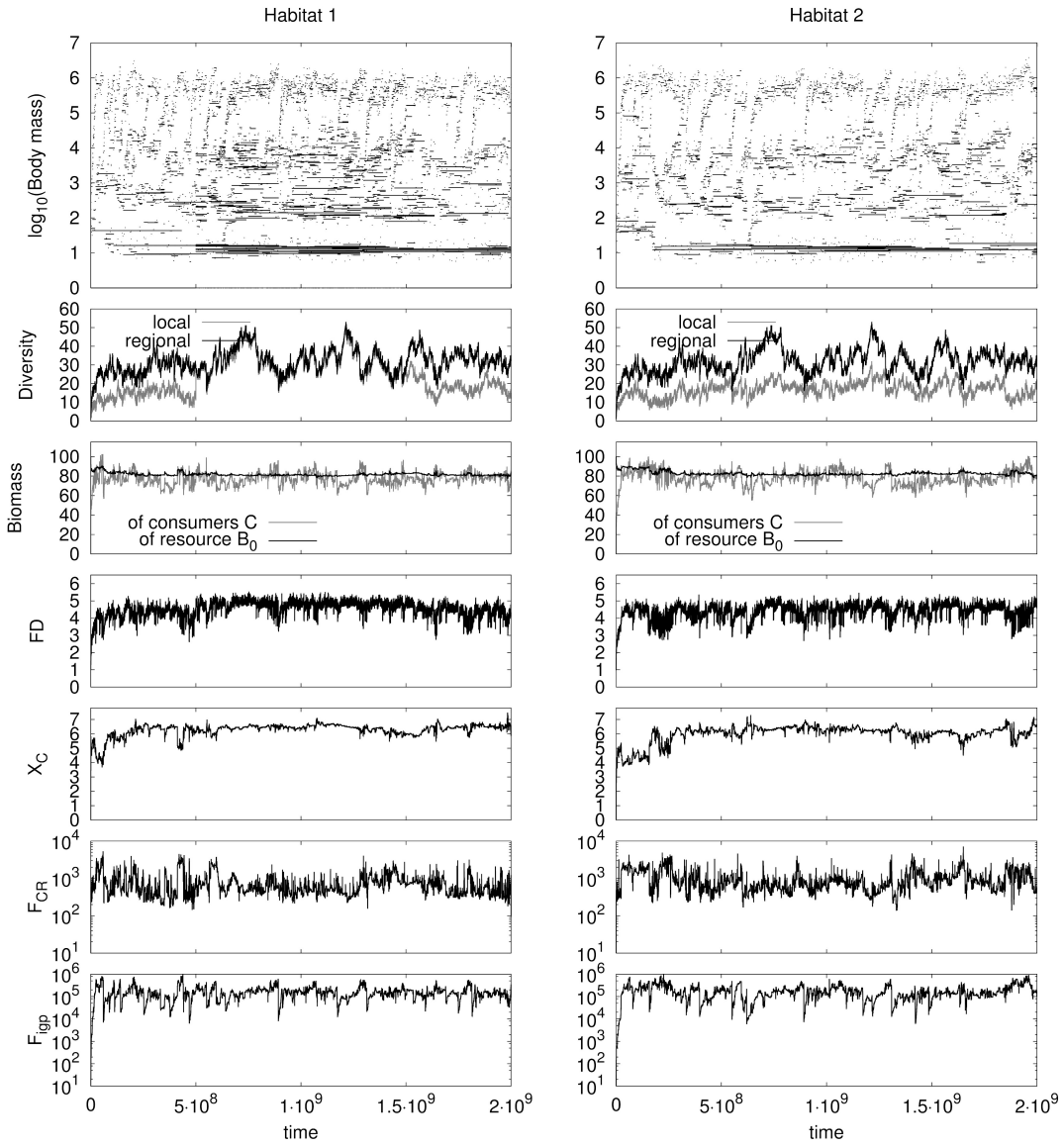

Figure 5.3.: An evolutionary metacommunity of two homogeneous habitats coupled via a weak, directed migration link from habitat 2 to habitat 1. The migration rate is $\mu = 10^{-5}$ in the time interval $5 \cdot 10^8 < t < 1.5 \cdot 10^9$ and zero otherwise.

diversity becomes equal to the local diversity again. The stronger the migration rate, the more native species are displaced. This can be seen in the difference between the regional diversity and the local diversity of habitat 2.

Those species that immigrate to habitat 1, but also stay viable in their home habitat 2, provide a continuous biomass flow into the immigration habitat 1. For rather small migration rates, the network in habitat 1 benefits from this biomass inflow and is able to support more species, as shown in fig. 5.3. In case of a strong migration rate, the network structure in habitat 1 is dominated by the structure in habitat 2, as shown in fig. 5.2. The increased local diversity can not be maintained without the biomass inflow due to immigration. As soon as the migration is switched off, an extinction event takes place and the network in habitat 1 reduces to its former size

and structure again. The measures of ecosystem functioning in habitat 1 remain mostly unchanged during the whole coupling and decoupling process.

In this directed migration scenario, no rescue effect as explained in the previous subsection is observed. Since the migration link is asymmetric, the rescue effect could only happen in the immigration habitat 1. However, many potential parent species with big body masses in habitat 1 do not have a suitable backup population in habitat 2. They are either natives of habitat 1 that do not migrate or they are natives of habitat 2 that cannot overcompensate the emigration losses in their home habitat. Thus, evolutionary suicide is still possible in this scenario.

5.4 More complex variants

As in section 3.3, I also discuss scenarios, where either the spatial landscape or the migration link is designed in a more complex way, in order to get a deeper understanding of the system. As an example of a more complex spatial landscape, I investigate migration between heterogeneous habitats, see subsection 5.4.1. The investigations in subsection 5.4.2 on adaptive and density dependent migration were performed by Stephanie Kulpe and Theresa Hofmann in the course of their bachelor theses [125, 126].

5.4.1 Heterogeneous habitats

Here, I introduce a scenario of two habitats that differ in the respiration rates mimicking for example the effect of different climate conditions. In the first habitat, the original respiration rate of $x_i = 0.314 \cdot m_i^{-0.25}$ is applied, whereas species in the second habitat suffer from an increased respiration rate of $x_i = 2 \cdot 0.314 \cdot m_i^{-0.25}$. This leads to a decreased amount of total biomass C in the system. Less biomass flows from lower to upper trophic levels leading to fewer viable trophic levels, fewer body mass clusters and hence to a decreased functional diversity. The maximum viable body mass is reduced by approximately one order of magnitude, as shown in fig. 5.5 and 5.4.

After coupling the two networks, we observe a mixture between the effects observed in the previous section. The species composition in both networks becomes identical as soon as migration is switched on, as with undirected migration between homogeneous habitats. However, the population sizes differ due to the differing respiration rates, leading to a persistent biomass flow, as with directed migration between homogeneous habitats. Typically, the migration is now directed from rather big populations in the more life-sustaining environment in habitat 1 to rather small populations in the more life-hostile environment in habitat 2.

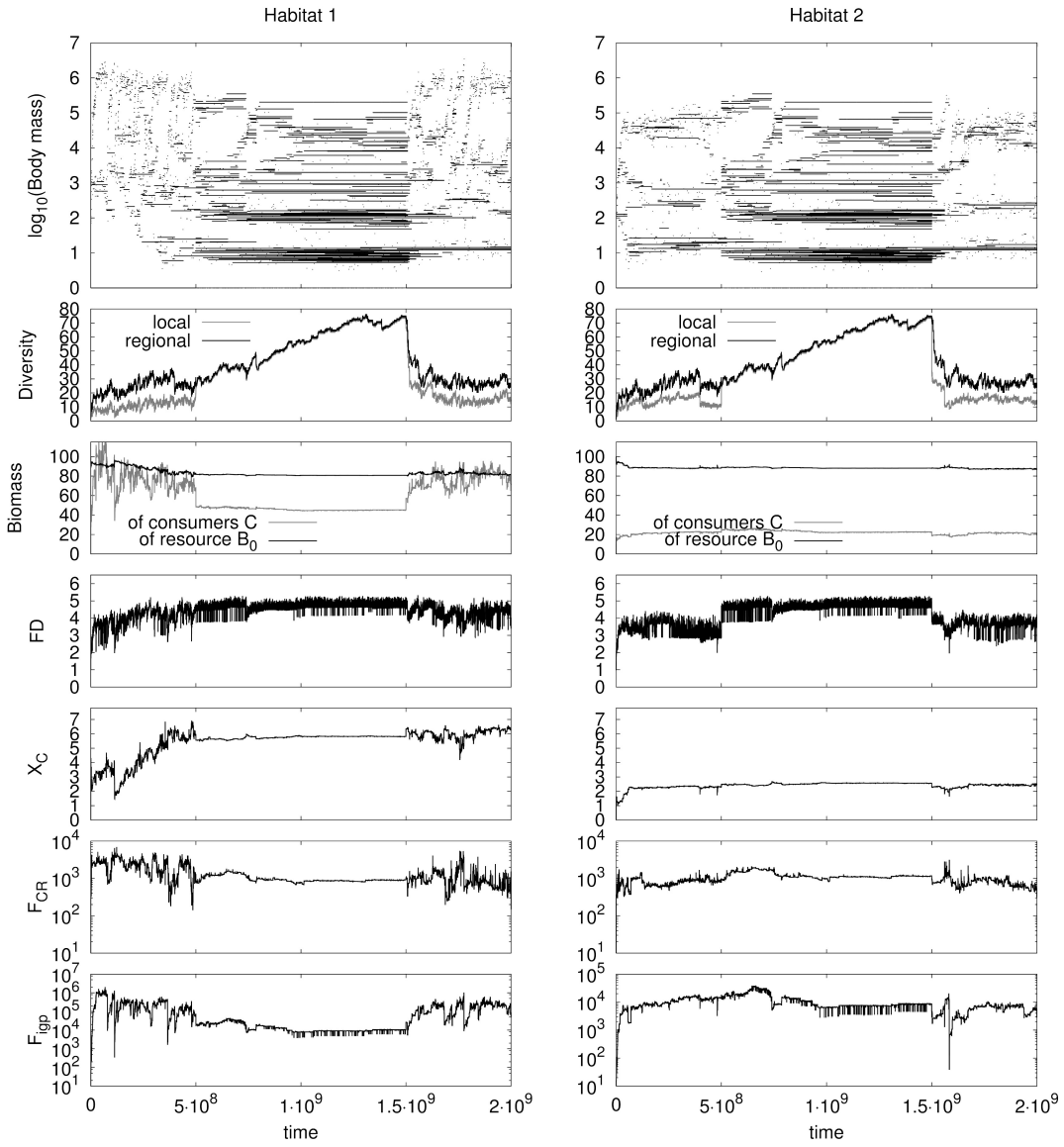

Figure 5.4.: An evolutionary metacommunity of two heterogeneous habitats coupled via a strong, undirected migration link. In habitat 1, the original respiration rate of $x_i = 0.314 \cdot m_i^{-0.25}$ is applied, whereas species in habitat 2 suffer from an increased respiration rate of $x_i = 2 \cdot 0.314 \cdot m_i^{-0.25}$. The migration rate is $\mu = 10^{-2}$ in the time interval $5 \cdot 10^8 < t < 1.5 \cdot 10^9$ and zero otherwise.

With a rather high migration rate of $\mu = 10^{-2}$ (fig. 5.4), we observe again the disappearance of species with big body masses due to the biomass loss of emigration in habitat 1. Also the stabilizing influence of the rescue effect, as explained in subsection 5.3.2, is visible in the increase of the diversity. The functional diversity in habitat 2 increases as well during the migration interval, since the additional biomass due to immigration is now also able to support species with body masses bigger than 5. After the migration is switched off, the food web in habitat 2 collapses immediately to its former size and the food web in habitat 1 recovers soon afterwards due to mutation events.

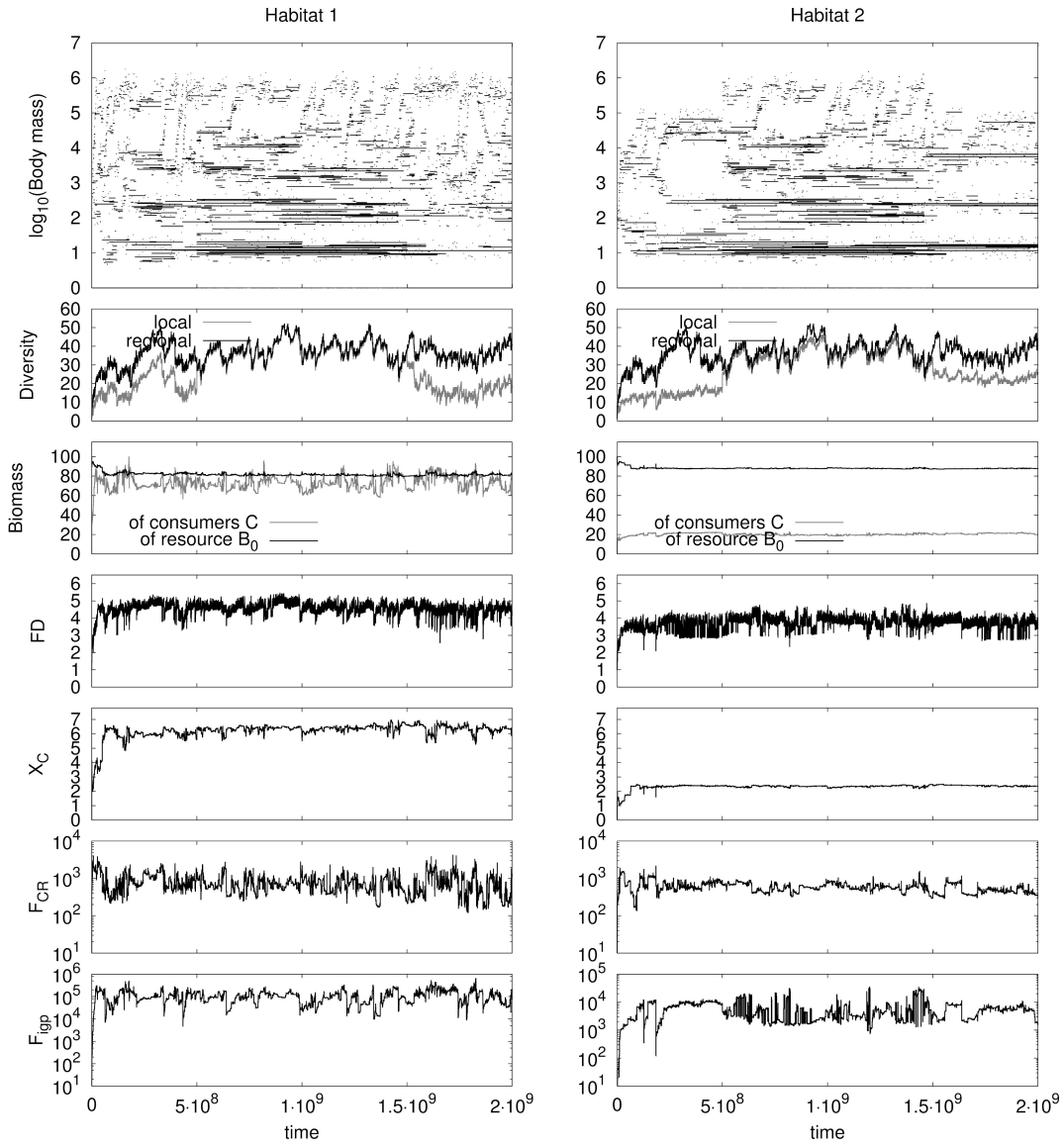

Figure 5.5.: An evolutionary metacommunity of two heterogeneous habitats coupled via a weak, undirected migration link. In habitat 1, the original respiration rate of $x_i = 0.314 \cdot m_i^{-0.25}$ is applied, whereas species in habitat 2 suffer from an increased respiration rate of $x_i = 2 \cdot 0.314 \cdot m_i^{-0.25}$. The migration rate is $\mu = 10^{-5}$ in the time interval $5 \cdot 10^8 < t < 1.5 \cdot 10^9$ and zero otherwise.

The lower the migration rates, the weaker are the described effects. With a rather small migration rate of $\mu = 10^{-5}$ (fig. 5.5), no rescue effect is observed. The population sizes of the immigration species in habitat 2 with body masses bigger than 10^5 stay far below their extinction threshold. Similar to the additional species observed as outcome 1 in section 3.2.2, they are not able to really establish themselves. Their population sizes are too small to become a parent species in this habitat. They are also too small to be a suitable backup population for parent species in habitat 1. Therefore, evolutionary suicide is possible and the species turnover is not influenced by the migration link in this case.

5.4.2 More complex types of migration

Before I performed the simulations presented in this chapter, I supervised two bachelor theses. Stephanie Kulpe [125] and Theresa Hofmann [126] compared diffusive migration to other types of migration in a setting of two homogeneous habitats. Both theses reveal very interesting results and helped immensely to get a first understanding of the behavior of the model in spatial landscapes.

However, the results are difficult to compare to my own results, due to the fact that a modified extinction criterion was in use. Instead of a critical individual density as in the original model version, a critical biomass density as in the model by Loeuille and Loreau was applied. At first sight, this is only a minor change and it can even be intuitively motivated, as will be discussed in subsection 6.2.1. However, after these two theses were finished, I realized that this seemingly minor change does in fact have a major impact on the resulting networks. Nevertheless, some results, which seem to be independent of the extinction rule, are explained in the following two subsections.

Adaptive migration

Stephanie Kulpe implemented adaptive migration, where the migration rate of a species is proportional to its growth rate if this growth rate is negative and zero otherwise, according to equation 3.3. She focused on directed migration, where only species from habitat 2 are able to migrate to habitat 1 [125]. The rescue effect is naturally excluded in this scenario, because the migration rate depends only on the local situation in habitat 2.

This type of migration is fundamentally different from diffusive migration. Like the model by Loeuille and Loreau, this model also typically approaches fixed points, where all growth rates and hence all migration rates are zero. However, the repeated emergence of new mutants disturb the system and after each successful mutation, the system approaches a new fixed point. Therefore, migration is limited in time to these periods of network restructuration.

Species that become extinct due to the emergence of a new mutant in habitat 2 have the highest migration rates and therefore the best chances to become established in habitat 1. Other species, that become disturbed but not extinct, have much smaller migration rates and therefore worse chances to become established. They reappear again and again with tiny population sizes in habitat 1, whenever their populations in their home habitat 2 is disturbed by a new mutant.

In summary, adaptive migration influences the species composition, but network properties like the fraction of species per trophic levels or the amount of biomass per trophic level are independent of this type of migration. This is due to the fact

that there is no constant biomass flow from habitat 2 to habitat 1 and consistent with the results of Eva Marie Weiel, see subsection 3.3.3.

Density dependent migration

Theresa Hofmann implemented a type of density dependent migration between both habitats, according to the work of Florian Schwarzmüller [126, 57]. The basic idea of this migration type is that the biomass density of a species in a habitat is directly related to several emigration triggers such as intra-specific competition or food availability. The emigration rate of a species i is thus assumed to follow a sigmoidally increasing relationship with its biomass density $B_{i,h}$ on habitat h:

$$\mu_{i,h\to h'} = \frac{B_{i,h}^2}{\left(B_{M_i}\left(1-\frac{\mu_{max}}{2}\right)^{-1}\right)^2 + B_{i,h}^2} \cdot \mu_{max}. \tag{5.7}$$

B_{M_i} is the mean biomass density of species i. For high biomass densities, this function saturates at μ_{max}. Theresa Hofman varied the value of μ_{max} between 0.5 and 10^{-7}.

A significant difference between diffusive and density dependent migration can be observed in a situation of directed migration between the two habitats. We have observed in fig. 5.2 that with strong diffusive migration, species in habitat 2 become extinct due to the biomass flow to habitat 1. With density dependent migration, most species in habitat 2 survive the onset of migration. Their population size is reduced until their migration rates are so small that they can be overcompensated. Small populations consume less resources. Therefore, new mutants can establish themselves. The effect can lead to a significantly increased regional diversity without a dramatic change in the functional diversity.

5.5 Discussion

One first striking difference between the metacommunities discussed here and the metacommunities based on the model by Loeuille and Loreau (chapter 3) is that the additional mini-populations of outcome 1 are not observed within homogeneous habitats. With the new model and undirected diffusive migration, the networks become identical. This corresponds to outcome 2, but is here independent from the migration rate.

This is due to the different design of the competition term. In the model by Loeuille and Loreau, competition is exclusive, meaning that usually only one of two competing species survives. Thus, the box-shaped competition range specifies the equally distributed viable niches within a trophic level on the body mass axis. The

competition with native species limits the population sizes of immigrating species so that additional mini-populations can be observed.

In the new model, competition is modeled as a term in the denominator of the consumption rate. High competition values lead to less predation input, but not to a loss of biomass. The viable niches within a trophic level (and hence the number of species per trophic level) are not fixed as in the first model. They depend on the current situation in the food web, e.g. on the biomass densities of the competitor species and hence on their competition pressure. New viable niches can occur within a given trophic level, when all species within that level experience decreasing population sizes, for example according to emigration losses as observed in habitat 2 in fig. 5.2. The network structure therefore strongly depends on the current spatial situation, in contrast to the results in chapter 3.

Even though the additional mini-populations of outcome 1 do not occur within homogeneous habitats, something similar does occur within heterogeneous habitats. The species compositions become identical, but the dispersal is directed from the more life-sustaining environment in habitat 1 to the more life-hostile environment in habitat 2. Species with big body masses immigrate to habitat 2, but they are scarcely able to establish themselves. The mechanism is similar to outcome 1, where the biomass gain due to immigration is not sufficient to overcompensate the biomass loss due to the competition with natives. Here, it is not sufficient to overcompensate the increased respiration rate. The effect is the same: The populations of the immigrants stay small and they disappear as soon as the migration is switched off.

Apart from the emergence of new viable niches due to changes in the biomass densities, also another effect occurred here, but was not observed with the model by Loeuille and Loreau, namely the rescue effect. Here, it prevents evolutionary suicide of species with big body masses. This stabilizes the upper trophic levels and therefore the whole network, leading to the complete filling of all available viable niches and hence to an increase of the diversity and to more complex networks than in isolated habitats. This corresponds to the ideas of Gravel et al. [69] and Pillai et al. [70], who also stated that space might be the key to the diversity-stability debate as explained in subsection 1.2.2.

The rescue effect and its influences on the network evolution could not be observed in the model by Loeuille and Loreau, since the resulting networks are already very stable and since all viable niches are and remain occupied, as explained in chapter 2. However, the rescue effect is well known from other studies [134, 135, 136]. For example, Plitzko and Drossel constructed niche networks and placed them on several patches in a (non-evolving) metacommunity [137]. The population sizes were initiated with random values, which led to random extinction events in case of isolated habitats or very small migration rates. Intermediate migration rates led to the re-occupation of habitats and therefore to the survival of more species. This is measured as a significantly (but not dramatically) in-

creased value of the robustness, which is the average proportion of species that are present after the system has reached an attractor. With the simulations presented in this chapter, I show that the rescue effect, which actually concerns only very few species, can in fact have a much more dramatic influence on the network structure as a whole, when evolution and species turnover are taken into account.

The investigations of evolutionary metacommunities presented in this chapter are still work in progress. More simulations of the scenarios presented here are needed for a statistically thorough analysis in order to quantitatively describe the observed effects. Also longer simulations are needed in order to discuss the long-term behavior of coupled food webs. The scenarios presented here (only two habitats, the same spatial topology for all species, the same migration type and rate for all species, etc) are certainly oversimplified and the results can therefore probably not be readily transferred to real ecosystems.

However, these first approaches already provide interesting insights. Dobson et al. stated that species from high trophic levels react most sensitively to a changing environment [3]. The authors therefore recommend that conservation ecology should aim at the preservation of top predators, since they serve as an important alarm bell. If ecosystems can maintain healthy populations of top predators, it is likely that they will also contain healthy populations of many lower level species that perform a diversity of ecosystem services. My results confirm that the top trophic level is extremely sensitive to changes in the spatial environment. Moreover, I could show that changes in this level, although they are rather small compared to the network as a whole, already have a massive impact on the evolving network.

As Loreau highlighted, evolutionary food web models potentially provide major contributions to the BEF debate [124], because both short-term and long-term responses of ecosystems to changes in their environment can be taken into account. Here I analyzed a changing spatial topoloy as one example of environmental changes. In this context I found two effects that arise from the interplay of evolution and dispersal, namely the rescue effect that prevents evolutionary suicide on the one hand and the increase of diversity due to the emergence of new niches due to emigration on the other. Both effects influence the food webs in the metacommunity dramatically. They could not be observed or explained in previous studies that disregard either evolution or dispersal or both.

6 Conclusion

In the following section a summary of my results can be found. Some ideas for further research topics are subsequently presented in section 6.2.

6.1 Summary

In this thesis, I investigated evolutionary metacommunities. The food webs analyzed here are neither static nor isolated, in contrast to various previous studies. Instead, they are modeled as "evolutionary networks of networks" that take both species turnover and spatial influences into account. I used two different evolutionary food web models to describe the local dynamics within one habitat. Metacommunities built with the model by Loeuille and Loreau are able to generate several results that were already known before from non-evolving (!) metacommunity studies. For example, this includes the decrease of the global diversity with an increasing migration rate, as explained in chapter 3. Two outcomes were observed in a wide range of spatial settings, namely either additional mini-populations in case of small migration rates or mostly identical networks in case of high migration rates. A similar behavior is known from plants (outcome 1) and birds (outcome 2) analyzed in an island study by Sax et al. [99].

It is known from several studies that the combination of space and evolution leads to phenomena that can not be observed or explained when either evolution or space is considered. Examples for such studies were mentioned in subsection 1.2.5 and throughout this thesis. Hence, it is very surprising at first sight that the same results, that were initially known from metacommunities with static species compositions, are now also observed in an evolutionary context. However, on second sight, it is less surprising when considering the peculiarities of this particular model.

The resulting networks are remarkably stable, as explained in chapter 2. Species are characterized by their body mass, which is the only evolving trait. Even if a mutant species is able to successfully displace its parent species, it does not change the network structure, since parent and mutant species usually have similar body masses and hence a similar function in the network. This mechanism is still at work when several habitats are coupled, which explains the similar results from this study and from non-evolving metacommunity studies. However, the species composition can be dependent on the spatial setting even if the network structure is not (e.g. with adaptive migration).

A more realistic evolutionary food web model has been introduced in chapter 4. It is based on the results presented in chapter 2: A successful evolutionary food web model needs to fulfill two conditions, which are the evolution of more traits in addition to body mass on the one hand and reasonable restrictions for each

evolving trait on the other. The resulting food webs are not only more realistic than the results by Loeuille and Loreau, they also show a continuous species turnover. This turnover is triggered via a specialization-extinction circle on the one hand and evolutionary suicide on the other. The model supports the hypothesis that mass extinctions need external drivers, but that smaller extinction events are an intrinsic property of ecosystems.

The model also provides answers to other urgent questions in ecology, for example concerning climate change, biodiversity and ecosystem functioning (BEF) and metacommunity theory. The latter two topics are considered in chapter 5. Since the isolated model without space already shows a broader range of phenomena than the model by Loeuille and Loreau, it is no surprise that the same is true in a spatial context. The viable niches are less static and the capacities of the trophic levels strongly depend on the current situation in the network. The food web structures react to changes in the spatial environment and the model is therefore able to show not only short-term but also long-term effects.

I found two phenomena that arise from the interplay between evolutionary and spatial dynamics. The rescue effect leads to a stabilization of the top species and therefore of the whole network. Decreasing populations (for example due to emigration losses) lead to the emergence of new viable niches. Both effects lead to an increasing regional diversity.

These phenomena can not be observed or explained with previous metacommunity approaches, where species turnover is not considered. The metacommunity scenarios presented in chapter 5 provide a good impression of the possible long-term effects of habitat coupling and de-coupling and of how dramatic these effects might be. The specific outcomes may of cause be due to the specific design of the model and the spatial settings. Other models and spatial settings with other local interaction and dispersal rules will probably lead to different results. However, the fact that the interplay of both mechanisms leads to dramatic changes is certainly transferable to other studies. This strongly indicates that an increased focus on the interplay of the evolutionary and the spatial perspective on food webs is necessary. A deeper understanding of the mechanisms that stabilize ecosystems despite changes in the species composition and the spatial environment is urgently needed before habitat fragmentation, habitat isolation and other interventions lead to irreversible consequences.

6.2 Outlook

Some ideas for further research were already mentioned in the discussion parts of the individual chapters and will not be repeated here. Instead, I would like to highlight three important topics that might represent the next steps in understanding evolutionary metacommunities.

6.2.1 How dead is dead?

The new evolutionary food web model presented in chapter 4 uses a critical individual density as the extinction criterion for all species. Without a deeper understanding of the mechanisms that drive species towards extinction, this criterion represents a lowest boundary: Assuming sexual reproduction, two individuals are the absolute minimum of a viable population. However, two elephants in an area as big as Darmstadt are able to find each other, whereas the same task is probably more difficult for two mice.

A perhaps more intuitive extinction threshold would be a critical density of two individuals per home range H, which is the typical area, which one individual is able to roam through during its lifetime. Jetz et al. suggested that the home range scales approximately linear with body mass m: $H \propto c \cdot m^1$ [138], which leads to a constant critical biomass B_{crit} density for all species:

$$B_{\text{crit}} = \frac{2}{H} \cdot m = \frac{2}{c \cdot m^1} \cdot m = \frac{2}{c}$$

Theresa Hofmann and Stephanie Kulpe used this alternative extinction criterion in their bachelor theses, as mentioned in section 5.4.2. Recent test simulations with this criterion resulted in surprisingly different results. Initially, the networks emerge and evolve in the same way as in the simulations performed with the original extinction criterion. However, in case of long time scales and in contrast to the simulations presented in this work, the extinction events become rarer and smaller over time. Moreover, the network structure differs significantly from the networks presented in this work, with many species in high trophic levels and only a few species in low trophic levels.

With the original extinction criterion, species in high trophic levels and with big body masses are typically close to their extinction threshold. As a consequence, they are at risk of going extinct during a mutation process, since the mutant's biomass is always derived from the parent species. In this case, even if the mutant is unable to establish itself, the parent species goes extinct, which mimics evolutionary suicide [32]. The loss of those top-predators creates new niches or changes the capacity of already existent niches and thus furthers the continuous species turnover in the whole network. With the alternative extinction criterion, the same species would

have a much lower extinction threshold. The risk of going extinct during a mutation event is thus smaller, resulting in less species turnover and more species on higher trophic levels.

Not only the extinction criterion is important, but also the exact value of the threshold. Smaller or larger values can lead to the survival of more or less species and hence to networks of different sizes. Additionally, it may even be important how often the extinction criterion is applied. Imagine a mutant in a metacommunity that is initialized in one habitat at its extinction threshold. When applying the criterion at each time step, such a mutant would hardly have a chance to establish itself due to emigration losses. However, it might be viable, if it is able to establish itself in other habitats and remigrates at some point. Thus, when checking for example at each mutation event, more mutants can survive.

The above mentioned observations suggest that the extinction criterion plays a highly important role in evolutionary food web models. So far, this issue receives very little attention. Many authors use some "small" extinction threshold and argue that the exact value or the characteristic of this threshold is not important since all populations are usually much bigger. This argument might be reasonable for static network structures. However, it is inappropriate for evolutionary food web models, since new species keep on entering the system until some species are close to their extinction threshold. For example, Loeuille and Loreau simply used a constant critical biomass density for all species [1] and concentrated on their analysis of other model components. A justification for this extinction rule (or a motivation via home ranges as explained above) is lacking in the original article. The same holds for the evolutionary niche model [45].

A thorough analysis of realistic mechanisms driving a species towards extinction and of the influences of different extinction rules on food webs is definitely necessary in order to evaluate the reliability and capability of evolutionary food web models.

6.2.2 Increasing spatial complexity

So far, I have concentrated on rather simple spatial landscapes of only two coupled habitats. Larger systems with more realistic (which means more complex) spatial topologies would probably lead to more realistic results, which are perhaps able to reflect the enormous range of different outcomes observed in nature.

However, including more and more "realistic" features of ecosystems is problematic. There are basically two types of modeling: Either you wish to produce as realistic results as possible, or you wish to build a model that is as simple as possible but able to explain a certain phenomena. Trying to cover the complexity of nature in metacommunity models bears the risk of building models that are too complex to be understandable. Such models might be valuable for reproducing data sets or for forecasting, but they are useless for generating a basic understand-

ing. I therefore concentrate only on a few selected ideas of an increased spatial complexity that might provide useful insights.

Fragmented landscapes in nature (e.g. archipelagos, fragmented forests, systems of waterbodies etc) usually consist of more than two habitats. Increasing the number of habitats is therefore the first idea of an increased spatial complexity. Ristl et al. found that the spatial topology has a significant influence on the food webs [58]. In this context, not every possible spatial topology is meaningful. For example, a fully connected spatial network seems to be inappropriate, since connections to habitats far away should be weaker than connections to closer habitats. Migration links should therefore depend on the distance between two habitats, as for example considered by Schwarzmüller and Brose [57]. Species dependent topologies could also be of interest, since the same distance can be a short hop for one species and insuperable for another.

As a first approach towards larger evolutionary metacommunities, it would be interesting to study spatial topologies of 5 habitats. This is still small enough to be easy to handle, but yet complex enough to generate several possible spatial topologies. Plitzko and Drossel analyzed niche networks on several 5-patch-topologies and stated that they have a significant impact on the robustness of metacommunities [137]. However, their investigations are not able to show the long-term influences of the spatial topologies. They found that especially the star topology furthers the robustness, since the central habitat accommodates a huge reservoir of biomass. In an evolutionary context, this increased biomass reservoir might lead to the emergence of new viable niches and therefore to an increase of the diversity.

Instead of x habitats building a certain spatial topology, it might also be enlightening to simply consider a lattice of habitats. Here, the concept of species dependent migration rates can easily be implemented: Species with a small migration range can only migrate to next neighbor habitats, whereas other species (e.g. birds) might also be able to migrate to habitats far away. A one dimensional scenario of many habitats in a row would be a nice link to the work of Daniel Ritterskamp, who is currently analyzing food webs in a one dimensional continuous space in the course of his PhD thesis.

However, the increase of complexity via an increase of the number of habitats leads to higher computational effort. The evolutionary food web model presented in this thesis is only suitable for systems with few habitats. Nevertheless, the spatial complexity can also be increased without increasing the number of habitats.

A first idea would be to increase the complexity of the migration link. In this thesis, I already discussed adaptive and biomass dependent migration rates as alternatives to diffusion. But even in these approaches, the same type of migration is considered for all species in the system. In reality, several types of migration naturally coexist. An approach of rather random movement for lower level species and rather adaptive movement for higher level species, that are able to evaluate and to react to their current situation, might be interesting.

A higher level of complexity can also be introduced via different properties of the habitats in a metacommunity. In chapter 5 we have seen that especially the migration between heterogeneous habitats leads to interesting results. Metacommunities with heterogeneous landscapes have already been studied by several authors - but usually with static species compositions. In an evolutionary context, the food webs are able to adapt to the local situation leading to different results compared to previous studies and therefore to new insights.

6.2.3 A minimalistic but realistic evolutionary food web model

Unfortunately, the program runtime increases dramatically with the number of habitats and makes the analysis of large metacommunities a challenging task. To simulate a food web of S species, the solver has to deal with a $(S \times S)$ - matrix. Two habitats with two different sets of species would accordingly correspond to a $(2S \times 2S)$ - matrix, etc.

One idea to overcome this issue is to use a reduced version of the model presented in this work. Tobias Rogge started his master thesis in August 2014 and is currently working on the details of such a minimalistic model. The evolutionary algorithm and the characterization of the species is very similar to the original model. However, population dynamics is not explicitly taken into account, which leads to an enormous reduction of program runtime. All populations and interaction links are regarded to be either existent or absent. The effects that typically arise from population dynamics are captured instead by a "survival index" that depends on the trophic position of the species, on the number of ingoing and outgoing links and on the number of competitors.

First promising results suggest that it is possible to obtain similar network structures as with the original model. Realistic network structures emerge and evolve with very little computational effort. This minimalistic model might therefore be a very powerful tool to evaluate statistical properties of metacommunities over long timescales, over a large parameter space, and for a large number or a whole lattice of coupled habitats.

A Appendix

A.1 Empirical data

We used a recently compiled collection of empirical food webs from a variety of different ecosystems (estuary, river, lake, marine, terrestrial) to test the evolving model networks against [112], see fig. 4.5 and 4.6. The data was provided by Christoph Digel and Jens Riede. This data set contains 65 food webs with species numbers between 27 and 492. We did not evaluate all 65 food webs, but only the 51 networks for which we also had the body masses of all species. The list of empirical food webs used is given in table A.1.

A.2 Cutoff for weak links

Both evolutionary food web models discussed in this thesis define feeding links between species using Gaussian feeding kernels. These feeding kernels extend in principle over the whole niche axis. To obtain meaningful network structures, very weak links have to be cut off. We removed all links that contribute less than a certain fraction of the average link to the total resources of the respective consumer. Here, I demonstrate the effects of different cutoff values (fig. A.1). I also show how the networks generated with the model by Loeuille and Loreau [1] are affected when this cutoff criterion is applied. In general, a lower cutoff value leads to less links being removed and thereby to a higher connectance. This is accompanied by a lower fraction of top species, more species that are a part of feeding loops or that are cannibalistic, and overall more similar species (in terms of decreasing standard deviations of vulnerability and linkedness). Also, more links in the networks increase the clustering coefficient and decrease the characteristic path length. The networks that were generated with the model by Loeuille and Loreau overall look more realistic if our cutoff criterion is applied instead of the original one.

No.	and name as in [112]	ref.	No.	and name as in [112]	ref.
3	St. Mark's	[139]	33	Guadeloupe River	[140]
4	Ythan2010	[141]	34	Los Gatos Creek	[140]
6	Alford Lake	[142]	35	Los Trancos Creek	[140]
7	Balsam Lake	[142]	36	San Francisquito Creek	[140]
8	Beaver Lake	[142]	37	Saratoga Creek	[140]
9	Big Hope Lake	[142]	38	Steverson Creek	[140]
10	Bridge Brook Lake	[142]	39	Blackrock	[140]
11	Chub Pond	[142]	41	Ross	[143]
12	Connery Lake	[142]	42	Penetetia Creek	[140]
13	Hoel Lake	[142]	44	Canton	[143]
15	Stink Lake	[142]	45	Dempster	[143]
16	Little Rock Lake	[142]	47	Healy	[143]
17	Sierra Lakes	[144]	50	Stony	[143]
18	Skipwith Pond	[145]	51	Grand Caricaie Cl C1	[146]
19	Tuesday Lake	[147]	52	Coachella	[148]
21	Lough Hyne	[149]	53	EcoWeb 59	[150]
22	Mondego Zostera Meadows	[151]	54	EcoWeb 60	[150]
23	Caribbean Reef, small	[152]	56	Grand Caricaie Sn C2	[146]
25	Weddell Sea	[104, 23, 149]	59	Grand Caricaie Cm M2	[146]
26	Bere Stream	[153]	60	Simberloff_E1	[154]
27	Broadstone Stream	[155]	61	Simberloff_E2	[154]
28	Alamitos Creek	[140]	62	Simberloff_E3	[154]
29	Caldero Creek	[140]	63	Simberloff_E7	[154]
30	Corde Matre Creek	[140]	64	Simberloff_E9	[154]
31	Coyote Creek	[140]	65	Simberloff_ST2	[154]
32	Guadeloupe Creek	[140]			

Table A.1.: List of empirical food webs used to test the evolving model networks against, see fig. 4.5, 4.6 and A.1.

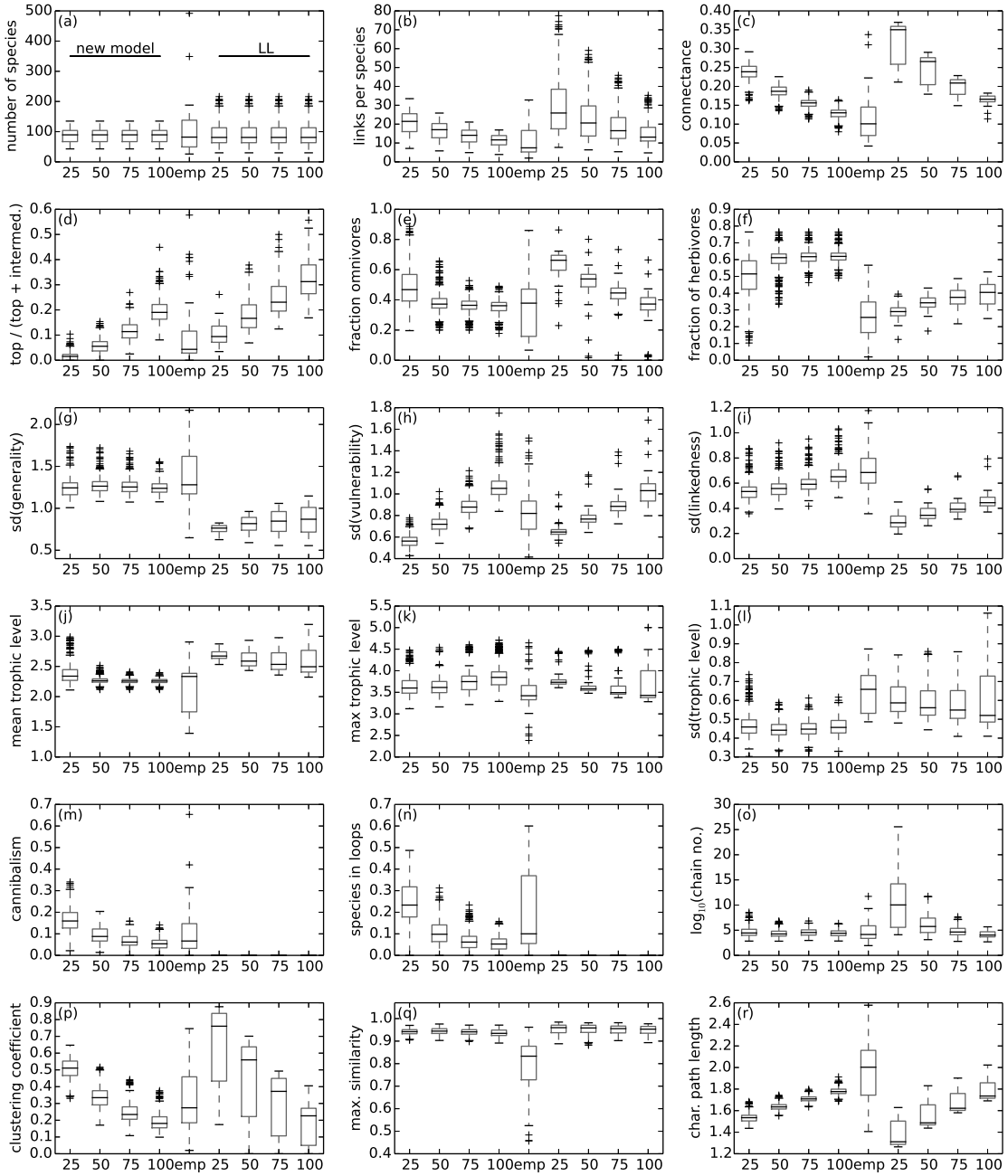

Figure A.1.: The influence of different cutoff threshold values. A link is regarded as absent if it contributes less than $x\%$ of the average link to the total resources of a consumer. The first four entries represent an average over the four main realizations of the new model. **emp**: Average over 51 empirical food webs. **LL**: Average over 75 simulations of the model of Loeuille and Loreau [1].

List of Figures

Bibliography

[1] Nicolas Loeuille and Michel Loreau. Evolutionary emergence of size-structured food webs. *PNAS*, 102(16):5761–5766, 2005.

[2] Charles Darwin and Gillian Beer. *The origin of species*. Oxford University Press Oxford, 1951.

[3] Andrew Dobson, David Lodge, Jackie Alder, Graeme S Cumming, Juan Keymer, Jacquie McGlade, Hal Mooney, James A Rusak, Osvaldo Sala, Volkmar Wolters, et al. Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology*, 87(8):1915–1924, 2006.

[4] Justin D. Yeakel, Mathias M. Pires, Lars Rudolf, Nathaniel J. Dominy, Paul L. Koch, Paulo R. Guimaraes, and Thilo Gross. Collapse of an ecological network in ancient egypt. *Proceedings of the National Academy of Sciences*, 111(40):14472–14477, 2014.

[5] Melanie Hagen, W Daniel Kissling, Claus Rasmussen, Marcus AM De Aguiar, Lee L Brown, Daniel W Carstensen, Alves-Dos Santos, Yoko L Dupont, Francois K Edwards, Paulo R Guimarães, et al. Biodiversity, species interactions and ecological networks in a fragmented world. *Advances in Ecological Research*, 46:89–210, 2012.

[6] Andrew Gonzalez, Bronwyn Rayfield, and Zoë Lindo. The disentangled bank: How loss of habitat fragments and disassembles ecological networks. *American Journal of Botany*, 98(3):503–516, 2011.

[7] DM Raup. Biological extinction in earth history. *Science*, 231(4745):1528–1533, 1986.

[8] Anthony D Barnosky, Nicholas Matzke, Susumu Tomiya, Guinevere OU Wogan, Brian Swartz, Tiago B Quental, Charles Marshall, Jenny L McGuire, Emily L Lindsey, Kaitlin C Maguire, et al. Has the earth's sixth mass extinction already arrived? *Nature*, 471(7336):51–57, 2011.

[9] Norman Myers and Andrew H Knoll. The biotic crisis and the future of evolution. *Proceedings of the National Academy of Sciences*, 98(10):5389–5392, 2001.

[10] Barbara Drossel and Alan J. McKane. *Modelling food webs, in Handbook of Graphs and Networks: From the Genome to the Internet*, chapter 10. Wiley-VCH Verlag GmbH & Co. KGaA, Weinheim, 2005.

[11] Barbara Drossel. Biological evolution and statistical physics. *Advances in Physics*, 50(2):209–295, 2001.

[12] Richard J. Williams and Neo D. Martinez. Limits to trophic levels and omnivory in complex food webs: Theory and data. *The American Naturalist*, 163(3):pp. 458–468, 2004.

[13] Garrick T Skalski and James F Gilliam. Functional responses with predator interference: viable alternatives to the holling type ii model. *Ecology*, 82(11):3083–3092, 2001.

[14] JE Cohen and CM Newman. A stochastic theory of community food webs: I. models and aggregated data. *Proceedings of the Royal society of London. Series B. Biological sciences*, 224(1237):421–448, 1985.

[15] Joel E Cohen, Frédéric Briand, and Charles M Newman. Community food webs. *Data and theory*, 1990.

[16] Richard J. Williams and Neo D. Martinez. Simple rules yield complex food webs. *Nature*, 404:180–182, 2000.

[17] Robert M. May. Will a large complex system be stable? *Nature*, 238(5364):413–414, 1972.

[18] Kevin Shear McCann. The diversity-stability debate. *Nature*, 405:228–233, 2000.

[19] P. Yodzis. The stability of real ecosystems. *Nature*, 289(5799):674–676, 1981.

[20] Peter C. de Ruiter, Anje-Margriet Neutel, and John C. Moore. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science*, 269(5228):1257–1260, 1995.

[21] Anje-Margriet Neutel, Johan A. P. Heesterbeek, and Peter C. de Ruiter. Stability in real food webs: Weak links in long loops. *Science*, 296(5570):1120–1123, 2002.

[22] Anje-Margriet Neutel, Johan A. P. Heesterbeek, Johan van de Koppel, Guido Hoenderboom, An Vos, Coen Kaldeway, Frank Berendse, and Peter C. de Ruiter. Reconciling complexity with stability in naturally assembling food webs. *Nature*, 449(7162):599–602, 2007.

[23] Ulrich Brose, Richard J. Williams, and Neo D. Martinez. Allometric scaling enhances stability in complex food webs. *Ecol. Lett.*, 9(11):1228–1236, 2006.

[24] R.J. Williams and N.D. Martinez. Stabilization of chaotic and non-permanent food-web dynamics. *Eur. Phys. J. B*, 38:297–303, 2004.

[25] Boris Kartascheff, Christian Guill, and Barbara Drossel. Positive complexity-stability relations in food web models without foraging adaptation. *J. Theor. Biol.*, 259(1):12–23, 2009.

[26] Michio Kondoh. Foraging adaptation and the relationship between food-web complexity and stability. *Science*, 299(5611):1388–1391, 2003.

[27] Satoshi Uchida and Barbara Drossel. Relation between complexity and stability in food webs with adaptive behavior. *J. Theor. Biol*, 247(4):713–722, 2007.

[28] Björn Christian Rall, Gregor Kalinkat, David Ott, Olivera Vucic-Pestic, and Ulrich Brose. Taxonomic versus allometric constraints on non-linear interaction strengths. *Oikos*, 120(4):483–492, 2011.

[29] Boris Kartascheff, Lotta Heckmann, Barbara Drossel, and Christian Guill. Why allometric scaling enhances stability in food web models. *Theor. Ecol.*, 3:195–208, 2010.

[30] L. Heckmann, B. Drossel, U. Brose, and C. Guill. Interactive effects of body-size structure and adaptive foraging on food-web stability. *Ecol. Lett.*, 15:243–250, 2012.

[31] Anna Eklöf, Matthew R Helmus, M Moore, and Stefano Allesina. Relevance of evolutionary history for food web structure. *Proceedings of the Royal Society B: Biological Sciences*, 279(1733):1588–1596, 2012.

[32] Kalle Parvinen. Evolutionary suicide. *Acta Biotheoretica*, 53(3):241–264, 2005.

[33] Jens O. Riede, Amrei Binzer, Ulrich Brose, Francisco de Castro, Alva Curtsdotter, Björn C. Rall, and Anna Eklöf. Size-based food web characteristics govern the response to species extinctions. *Basic and Applied Ecology*, 12(7):581 – 589, 2011.

[34] Amrei Binzer, Ulrich Brose, Alva Curtsdotter, Anna Eklöf, Björn C. Rall, Jens O. Riede, and Francisco de Castro. The susceptibility of species to extinctions in model communities. *Basic and Applied Ecology*, 12(7):590 – 599, 2011.

[35] Sonja B Otto, Björn C Rall, and Ulrich Brose. Allometric degree distributions facilitate food-web stability. *Nature*, 450(7173):1226–1229, 2007.

[36] Robert May. Unanswered questions in ecology. *Philos. Trans. R. Soc. London B Biol. Sci.*, 354(1392):1951–1959, 1999.

[37] GF Fussmann, M Loreau, and PA Abrams. Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology*, 21(3):465–477, 2007.

[38] Guido Caldarelli, Paul G. Higgs, and Alan J. McKane. Modelling coevolution in multispecies communities. *J. Theor. Biol.*, 193:345–358, 1998.

[39] Barbara Drossel, Paul G. Higgs, and Alan J. McKane. The influence of predator-prey population dynamics on the long-term evolution of food web structure. *J. Theor. Biol.*, 208(1):91–107, 2001.

[40] Barbara Drossel, Alan J. McKane, and Christopher Quince. The impact of nonlinear functional responses on the long-term evolution of food web structure. *J. Theor. Biol.*, 229(4):539–548, 2004.

[41] Carlos A. Lugo and Alan J. McKane. The robustness of the webworld model to changes in its structure. *Ecological Complexity*, 5(2):106–120, 2008.

[42] Carlos A. Lugo and Alan J. McKane. The characteristics of species in an evolutionary food web model. *J. Theor. Biol.*, 242(2):649–661, 2008.

[43] A.G. Rossberg, H. Matsuda, T. Amemiya, and K. Itoh. Food webs: Experts consuming families of experts. *J. Theor. Biol.*, 241(3):552 – 563, 2006.

[44] A.G. Rossberg, R. Ishii, T. Amemiya, and K. Itoh. The top-down mechanism for body-mass-abundance scaling. *Ecology*, 89(2):567–80, 2008.

[45] Christian Guill and Barbara Drossel. Emergence of complexity in evolving niche-model food webs. *J. Theor. Biol.*, 251(1):108–120, 2008.

[46] S Bauer and BJ Hoye. Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, 344(6179):1242552, 2014.

[47] Mikko Kivelä, Alex Arenas, Marc Barthelemy, James P. Gleeson, Yamir Moreno, and Mason A. Porter. Multilayer networks. *Journal of Complex Networks*, 2(3):203–271, 2014.

[48] Priyanga Amarasekare. Spatial dynamics of foodwebs. *Annual Review of Ecology, Evolution, and Systematics*, 39:479–500, 2008.

[49] Mathew A Leibold, M Holyoak, N Mouquet, P Amarasekare, JM Chase, MF Hoopes, RD Holt, JB Shurin, R Law, D Tilman, et al. The metacommunity concept: a framework for multi-scale community ecology. *Ecology letters*, 7(7):601–613, 2004.

[50] Vincent Calcagno, François Massol, Nicolas Mouquet, Philippe Jarne, and Patrice David. Constraints on food chain length arising from regional metacommunity dynamics. *Proceedings of the Royal Society B: Biological Sciences*, 278(1721):3042–3049, 2011.

[51] Vincent AA Jansen. The dynamics of two diffusively coupled predator–prey populations. *Theoretical Population Biology*, 59(2):119–131, 2001.

[52] Andre M de Roos, Edward McCauley, and William G Wilson. Pattern formation and the spatial scale of interaction between predators and their prey. *Theoretical population biology*, 53(2):108–130, 1998.

[53] Tobias Reichenbach, Mauro Mobilia, and Erwin Frey. Mobility promotes and jeopardizes biodiversity in rock–paper–scissors games. *Nature*, 448(7157):1046–1049, 2007.

[54] Katia Koelle and John Vandermeer. Dispersal-induced desynchronization: from metapopulations to metacommunities. *Ecology Letters*, 8(2):167–175, 2005.

[55] Robert D Holt. Food webs in space: on the interplay of dynamic instability and spatial processes. *Ecological Research*, 17(2):261–273, 2002.

[56] Bernd Blasius, Amit Huppert, and Lewi Stone. Complex dynamics and phase synchronization in spatially extended ecological systems. *Nature*, 399(6734):354–359, 1999.

[57] Florian Schwarzmüller and Ulrich Brose. Energy fluxes in fragmented ecosystems: dynamic stability of tri-trophic food chains under nutrient enrichment and habitat isolation. under review.

[58] Konstantin Ristl, Sebastian J. Plitzko, and Barbara Drossel. Complex response of a food-web module to symmetric and asymmetric migration between several patches. *Journal of Theoretical Biology*, 354(0):54 – 59, 2014.

[59] Eric Tromeur, Lars Rudolf, and Thilo Gross. Impact of dispersal on the stability of metapopulations. under review, arXiv identifier 1305.2769.

[60] Delphine Legrand, Olivier Guillaume, Michel Baguette, Julien Cote, Audrey Trochet, Olivier Calvez, Susanne Zajitschek, Felix Zajitschek, Jane Lecomte, Quentin Bénard, et al. The metatron: an experimental system to study dispersal and metaecosystems for terrestrial organisms. *Nature methods*, 9(8):828–833, 2012.

[61] Jürg B. Logue, Nicolas Mouquet, Hannes Peter, and Helmut Hillebrand. Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology & Evolution*, 26(9):482 – 491, 2011.

[62] Steven J. Presley and Michael R. Willig. Bat metacommunity structure on caribbean islands and the role of endemics. *Global Ecology and Biogeography*, 19(2):185–199, 2010.

[63] Karl Cottenie, Erik Michels, Nele Nuytten, and Luc De Meester. Zooplankton metacommunity structure: regional vs. local processes in highly interconnected ponds. *Ecology*, 84(4):991–1000, 2003.

[64] Bart Haegeman and Michel Loreau. General relationships between consumer dispersal, resource dispersal and metacommunity diversity. *Ecology letters*, 17(2):175–184, 2014.

[65] K. S. McCann, J. B. Rasmussen, and J. Umbanhowar. The dynamics of spatially coupled food webs. *Ecology Letters*, 8(5):513–523, 2005.

[66] Nicolas Mouquet and Michel Loreau. Coexistence in metacommunities: The regional similarity hypothesis. *The American Naturalist*, 159(4):pp. 420–426, 2002.

[67] Nicolas Mouquet and Michel Loreau. Community patterns in source-sink metacommunities. *The American Naturalist*, 162(5):544–557, 2003.

[68] David Sloan Wilson. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology*, pages 1984–2000, 1992.

[69] Dominique Gravel, Elsa Canard, Frédéric Guichard, and Nicolas Mouquet. Persistence increases with diversity and connectance in trophic metacommunities. *PloS one*, 6(5):e19374, 2011.

[70] Pradeep Pillai, Andrew Gonzalez, and Michel Loreau. Metacommunity theory explains the emergence of food web complexity. *Proceedings of the National Academy of Sciences*, 108(48):19293–19298, 2011.

[71] Harold A Mooney and Elsa E Cleland. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences*, 98(10):5446–5451, 2001.

[72] Mark C Urban and David K Skelly. Evolving metacommunities: toward an evolutionary perspective on metacommunities. *Ecology*, 87(7):1616–1626, 2006.

[73] Mark C. Urban. Maladaptation and mass effects in a metacommunity: Consequences for species coexistence. *The American Naturalist*, 168(1):pp. 28–40, 2006.

[74] Mark C Urban, Mathew A Leibold, Priyanga Amarasekare, Luc De Meester, Richard Gomulkiewicz, Michael E Hochberg, Christopher A Klausmeier, Nicolas Loeuille, Claire De Mazancourt, Jon Norberg, et al. The evolutionary ecology of metacommunities. *Trends in Ecology and Evolution*, 23(6):311–317, 2008.

[75] Thiago Fernando L. V. B. Rangel, Jose Alexandre F. Diniz-Filho, and Robert K. Colwell. Species richness and evolutionary niche dynamics: A spatial pattern-oriented simulation experiment. *The American Naturalist*, 170(4):pp. 602–616, 2007.

[76] G. Szabó, G. and G. Fáth. Evolutionary games on graphs. *Physics Reports*, 446:97–216, 2007.

[77] Jordi Moya-Laraño, José Román Bilbao-Castro, Gabriel Barrionuevo, Dolores Ruiz-Lupión, Leocadio G Casado, Marta Montserrat, Carlos J Melián, and Sara Magalhães. Eco-evolutionary spatial dynamics: Rapid evolution and isolation explain food web persistence. *Eco-Evolutionary Dynamics*, 50:75–143, 2014.

[78] N Loeuille and MA Leibold. Ecological consequences of evolution in plant defenses in a metacommunity. *Theoretical population biology*, 74(1):34–45, 2008.

[79] Nicolas Loeuille and Mathew A. Leibold. Evolution in metacommunities: On the relative importance of species sorting and monopolization in structuring communities. *The American Naturalist*, 171(6):pp. 788–799, 2008.

[80] Nicolas Loeuille and Mathew A. Leibold. Effects of local negative feedbacks on the evolution of species within metacommunities. *Ecology Letters*, 17(5):563–573, 2014.

[81] Korinna T Allhoff and Barbara Drossel. When do evolutionary food web models generate complex structures? *J. Theor. Biol.*, 334:122 – 129, 2013.

[82] Daisuke Takahashi, Åke Brännström, Rupert Mazzucco, Atsushi Yamauchi, and Ulf Dieckmann. Cyclic transitions in simulated food-web evolution. *J. Plant. Interact.*, 6(2-3):181–182, 2011.

[83] Ugo Bastolla, Michael Lässig, Susanna C. Manrubia, and Angelo Valleriani. Biodiversity in model ecosystems, ii: Species assembly and food web structure. *J. Theor. Biol.*, 235:531–539, 2005.

[84] Katsuhiko Yoshida. Evolutionary dynamics of species diversity in an interaction web system. *Ecol. Modell.*, 163(1-2):131–143, 2003.

[85] Kei Tokita and Ayumu Yasutomi. Emergence of a complex and stable network in a model ecosystem with extinction and mutation. *Theor. Popul. Biol.*, 63(2):131–146, 2003.

[86] Åke Brännström, Nicolas Loeuille, Michel Loreau, and Ulf Dieckmann. Emergence and maintenance of biodiversity in an evolutionary food-web model. *Theoretical Ecology*, 4(4):467–478, 2011.

[87] Travis Ingram, Luke J. Harmon, and Jonathan B. Shurin. Niche evolution, trophic structure, and species turnover in model food webs. *Am. Nat.*, 174(1):56–67, 2009.

[88] Mark Galassi, Jim Davies, James Theiler, Brian Gough, Gerard Jungman, Michael Booth, and Fabrice Rossi. *Gnu Scientific Library: Reference Manual*. Network Theory Ltd., 3 edition, February 2003. ISBN 0954612078.

[89] Michael Lässig, Ugo Bastolla, Susanna C. Manrubia, and Angelo Valleriani. Shape of ecological networks. *Phys. Rev. Lett.*, 86:4418–4421, 2001.

[90] Anna Eklöf, Ute Jacob, Jason Kopp, Jordi Bosch, Rocio Castro-Urgal, Natacha P. Chacoff, Bo Dalsgaard, Claudio de Sassi, Mauro Galetti, Paulo R. Guimaraes, Silvia Beatriz Lomascolo, Ana M. Martin Gonzalez, Marco Aurelio Pizo, Romina Rader, Anselm Rodrigo, Jason M. Tylianakis, Diego P. Vazquez, and Stefano Allesina. The dimensionality of ecological networks. *Ecology Letters*, 16(5):577–583, 2013.

[91] Korinna T Allhoff, Eva Marie Weiel, Tobias Rogge, and Barbara Drossel. On the interplay of speciation and dispersal: An evolutionary food web model in space. *Journal of Theoretical Biology*, 366:46–56, 2015.

[92] Eva Marie Weiel. *Evolutionary food web model on two patches coupled by migration*. Master thesis, TU Darmstadt, October 2013.

[93] Tobias Rogge. *Influence of migration on an evolutionary food web model in a chain of patches*. Bachelor thesis, TU Darmstadt, August 2013.

[94] Dov F. Sax and Steven D. Gaines. Species diversity: from global decreases to local increases. *Trends in Ecology & Evolution*, 18(11):561 – 566, 2003.

[95] Lauri Oksanen, Stephen D. Fretwell, Joseph Arruda, and Pekka Niemela. Exploitation ecosystems in gradients of primary productivity. *The American Naturalist*, 118(2):pp. 240–261, 1981.

[96] Franck Courchamp, Jean-Louis Chapuis, and Michel Pascal. Mammal invaders on islands: impact, control and control impact. *Biological Reviews*, 78(3):347–383, 2003.

[97] Thomas H Fritts and Gordon H Rodda. The role of introduced species in the degradation of island ecosystems: A case history of guam 1. *Annual review of Ecology and Systematics*, 29(1):113–140, 1998.

[98] Don A Driscoll and David B Lindenmayer. Empirical tests of metacommunity theory using an isolation gradient. *Ecological Monographs*, 79(3):485–501, 2009.

[99] Dov F Sax, Steven D Gaines, and James H Brown. Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *The American Naturalist*, 160(6):766–783, 2002.

[100] Korinna Theresa Allhoff, Daniel Ritterskamp, Björn C. Rall, Barbara Drossel, and Christian Guill. Evolutionary food web model based on body masses gives realistic networks with permanent species turnover. under review, arXiv identifier 1409.3373.

[101] Constantin Beck. *Analysis of an evolutionary food web model*. Bachelor thesis, TU Darmstadt, June 2013.

[102] Markus Schiffhauer. *Analysis of an evolutionary food web model concerning different mutation rules*. Bachelor thesis, TU Darmstadt, November 2014.

[103] Jannis Weigend. *Analysis of different mutation rules in an evolutionary food web model*. Bachelor thesis, TU Darmstadt, November 2014.

[104] Ulrich Brose, Tomas Jonsson, Eric L. Berlow, Philip Warren, Carolin Banasek-Richter, Louis-Felix Bersier, Julia L. Blanchard, Thomas Brey, Stephen R. Carpenter, Marie-France Cattin Blandenier, Lara Cushing, Hassan Ali Dawah, Tony Dell, Francois Edwards, Sarah Harper-Smith, Ute Jacob, Mark E. Ledger, Neo D. Martinez, Jane Memmott, Katja Mintenbeck, John K. Pinnegar, Björn C. Rall, Thomas S. Rayner, Daniel C. Reuman, Liliane Ruess, Werner Ulrich, Richard J. Williams, Guy Woodward, and Joel E. Cohen. Consumer-resource body-size relationships in natural food webs. *Ecology*, 87(10):2411–2417, October 2006.

[105] Jens O. Riede, Ulrich Brose, Bo Ebenman, Ute Jacob, Ross Thompson, Colin R. Townsend, and Tomas Jonsson. Stepping in elton's footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecology Letters*, 14(2):169–178, 2011.

[106] James H Brown, James F Gillooly, Andrew P Allen, Van M Savage, and Geoffrey B West. Toward a metabolic theory of ecology. *Ecology*, 85(7):1771–1789, 2004.

[107] Peter Yodzis and S Innes. Body size and consumer-resource dynamics. *American Naturalist*, pages 1151–1175, 1992.

[108] J. R. Beddington. Mutual interference between parasites or predators and its effect on searching efficiency. *Journal of Animal Ecology*, 44(1):pp. 331–340, 1975.

[109] D. L. DeAngelis, R. A. Goldstein, and R. V. O'Neill. A model for tropic interaction. *Ecology*, 56(4):pp. 881–892, 1975.

[110] Marten Scheffer and Egbert H van Nes. Self-organized similarity, the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences*, 103(16):6230–6235, 2006.

[111] Robert M May. On the theory of niche overlap. *Theoretical Population Biology*, 5(3):297–332, 1974.

[112] Jens O Riede, Björn C Rall, Carolin Banasek-Richter, Sergio A Navarrete, Evie A Wieters, Mark C Emmerson, Ute Jacob, and Ulrich Brose. Scaling of food-web properties with diversity and complexity across ecosystems. *Advances In Ecological Research*, 42:139–170, 2010.

[113] Andrew P Allen, James F Gillooly, Van M Savage, and James H Brown. Kinetic effects of temperature on rates of genetic divergence and speciation. *Proceedings of the National Academy of Sciences*, 103(24):9130–9135, 2006.

[114] Mary E Power, David Tilman, James A Estes, Bruce A Menge, William J Bond, L Scott Mills, Gretchen Daily, Juan Carlos Castilla, Jane Lubchenco, and Robert T Paine. Challenges in the quest for keystones. *BioScience*, pages 609–620, 1996.

[115] Anna Eklöf and Bo Ebenmann. Species loss and secondary extinctions in simple and complex model communities. *Journal of Animal Ecology*, 75(1):239–246, 2006.

[116] Jarad P Mellard and Ford Ballantyne IV. Conflict between dynamical and evolutionary stability in simple ecosystems. *Theoretical Ecology*, pages 1–16, 2014.

[117] K Sneppen, P Bak, H Flyvbjerg, and M H Jensen. Evolution as a self-organized critical phenomenon. *Proceedings of the National Academy of Sciences*, 92(11):5209–5213, 1995.

[118] MEJ Newman and RG Palmer. Models of extinction: A review. *arXiv preprint adap-org/9908002*, 1999.

[119] David A Vasseur and Kevin S McCann. A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. *The American Naturalist*, 166(2):184–198, 2005.

[120] Amrei Binzer, Christian Guill, Ulrich Brose, and Björn C Rall. The dynamics of food chains under climate change and nutrient enrichment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1605):2935–2944, 2012.

[121] Jon Norberg, Mark C Urban, Mark Vellend, Christopher A Klausmeier, and Nicolas Loeuille. Eco-evolutionary responses of biodiversity to climate change. *Nature Climate Change*, 2(10):747–751, 2012.

[122] James C Stegen, Regis Ferriere, and Brian J Enquist. Evolving ecological networks and the emergence of biodiversity patterns across temperature gradients. *Proceedings of the Royal Society B: Biological Sciences*, page rspb20111733, 2011.

[123] James C. Stegen, Brian J. Enquist, and Regis Ferriere. Eco-evolutionary community dynamics: Covariation between diversity and invasibility across temperature gradients. *The American Naturalist*, 180(4):pp. E110–E126, 2012.

[124] Michel Loreau. Linking biodiversity and ecosystems: towards a unifying ecological theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1537):49–60, 2010.

[125] Stephanie Kulpe. *Adaptive migration between evolving food webs*. Bachelor thesis, TU Darmstadt, 2014.

[126] Theresa Hofmann. *Density dependent migration between evolving food webs*. Bachelor thesis, TU Darmstadt, 2014.

[127] J Emmett Duffy, Bradley J Cardinale, Kristin E France, Peter B McIntyre, Elisa Thébault, and Michel Loreau. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters*, 10(6):522–538, 2007.

[128] DU Hooper, FS Chapin III, JJ Ewel, A Hector, Pablo Inchausti, Sandra Lavorel, JH Lawton, DM Lodge, M Loreau, S Naeem, et al. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological monographs*, 75(1):3–35, 2005.

[129] Julia Reiss, Jon R. Bridle, Jose M. Montoya, and Guy Woodward. Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution*, 24(9):505 – 514, 2009.

[130] Bradley Cardinale, Emmett Duffy, Diane Srivastava, Michel Loreau, Matt Thomas, and Mark Emmerson. Towards a food web perspective on biodiversity and ecosystem functioning. *Studies*, 60(40):20, 2009.

[131] Florian D Schneider, Ulrich Brose, Björn C Rall, and Guill Christian. The dynamics of predator diversity and ecosystem functioning in complex food webs. *under review*.

[132] Deborah L Finke and Robert F Denno. Predator diversity dampens trophic cascades. *Nature*, 429(6990):407–410, 2004.

[133] Donald R. Strong. Are trophic cascades all wet? differentiation and donor-control in speciose ecosystems. *Ecology*, 73(3):pp. 747–754, 1992.

[134] A. Gonzalez, J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science*, 281(5385):2045–2047, 1998.

[135] Ilkka Hanski. Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society*, 42(1-2):17–38, 1991.

[136] James H Brown and Astrid Kodric-Brown. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, 58(2):445–449, 1977.

[137] Sebastian J. Plitzko and Barbara Drossel. The effect of dispersal between patches on the stability of large trophic food webs. *Theoretical Ecology*, accepted 2014.

[138] Walter Jetz, Chris Carbone, Jenny Fulford, and James H Brown. The scaling of animal space use. *Science*, 306(5694):266–268, 2004.

[139] Robert R Christian and Joseph J Luczkovich. Organizing and understanding a winter's seagrass foodweb network through effective trophic levels. *Ecological Modelling*, 117(1):99–124, 1999.

[140] K. Harrison. *Effects of Land Use and Dams on Stream Food Web Ecology in Santa Clara Valley, California 127*. Thesis, San Francisco State University, 2003.

[141] Joel E Cohen, Daniella N Schittler, David G Raffaelli, and Daniel C Reuman. Food webs are more than the sum of their tritrophic parts. *Proceedings of the National Academy of Sciences*, 106(52):22335–22340, 2009.

[142] Karl Havens. Scale and structure in natural food webs. *Science*, 257(5073):1107–1109, 1992.

[143] Townsend, Thompson, McIntosh, Kilroy, Edwards, and Scarsbrook. Disturbance, resource supply, and food-web architecture in streams. *Ecology Letters*, 1(3):200–209, 1998.

[144] Sarah Harper-Smith, Eric L Berlow, Roland A Knapp, Richard J Williams, and Neo D Martinez. Communicating ecology through food webs: visualizing and quantifying the effects of stocking alpine lakes with trout. *Dynamic food webs: multispecies assemblages, ecosystem development, and environmental change*, pages 407–423, 2005.

[145] Philip H Warren. Spatial and temporal variation in the structure of a freshwater food web. *Oikos*, pages 299–311, 1989.

[146] Marie-France Cattin Blandenier. *Food web ecology: models and application to conservation*. PhD thesis, Université de Neuchâtel (Suisse), 2004.

[147] Tomas Jonsson, Joel E Cohen, and Stephen R Carpenter. Food webs, body size, and species abundance in ecological community description. *Advances in ecological research*, 36:1–84, 2005.

[148] Gary A Polis. Complex trophic interactions in deserts: an empirical critique of food-web theory. *American naturalist*, pages 123–155, 1991.

[149] Ute Jacob. *Trophic dynamics of Antarctic shelf ecosystems: food webs and energy flow budgets*. PhD thesis, Universität Bremen, 2005.

[150] J.E. Cohen. *Ecologists' Co-operative Web Bank [ECOWeb]. Machine-Readable Database of Food Webs*. Rockefeller University, New York, 1989.

[151] Joana Patrício and João Carlos Marques. Mass balanced models of the food web in three areas along a gradient of eutrophication symptoms in the south arm of the mondego estuary (portugal). *ecological modelling*, 197(1):21–34, 2006.

[152] Silvia Opitz. *Trophic interactions in Caribbean coral reefs*. Number 1085. WorldFish, 1996.

[153] Guy Woodward, Georgia Papantoniou, François Edwards, and Rasmus B Lauridsen. Trophic trickles and cascades in a complex food web: impacts of a keystone predator on stream community structure and ecosystem processes. *Oikos*, 117(5):683–692, 2008.

[154] Daniel S Simberloff and Lawrence G Abele. Island biogeography theory and conservation practice. *Science*, 191(4224):285–286, 1976.

[155] Guy Woodward, Dougie C Speirs, Alan G Hildrew, and C Hal. Quantification and resolution of a complex, size-structured food web. *Advances in ecological research*, 36:85–135, 2005.

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Education

since 2011	**Technical University Darmstadt, Germany**
	Ph.D. candidate in the group of Prof. B. Drossel
2005-2011	**Philipps-University Marburg, Germany**
	09/2011 diploma in physics (1.3)
	Thesis (1.0): "A directed percolation model for turbulence spreading" In the group of Prof. B. Eckhardt
	03/2008 Intermediate diploma (1.25)
2008-2009	**Budapest University of Technology and Economics, Hungary**
	Erasmus scholarship
2005	**Walram-Gymnasium Menden (Sauerland), Germany**
	Abitur (2.1)

Teaching experience

Supervised master theses

2014 **Tobias Rogge** (started in August)

2013 **Eva Marie Weiel** [92]:
"Evolutionäres Nahrungsnetzmodell auf zwei durch Migration gekoppelten Habitaten"

Supervised bachelor theses

2014 **Theresa Hofman** [126]:
"Dichteabhängige Migration zwischen evolvierenden Nahrungsnetzen"

Stephanie Kulpe [125]:
"Adaptive Migration zwischen zwei evolvierenden Nahrungsnetzwerken"

2013 **Jannis Weigend** [103]:
"Untersuchung verschiedener Vererbungsregeln in einem evolutionären Nahrungsnetzmodell"

Markus Schiffhauer [102]:
"Untersuchung eines Nahrungsnetzmodells (Variation der Mutationsregel)"

Constantin Beck [101]:
"Untersuchung eines evolutionären Nahrungsnetzmodells"

Tobias Rogge [93]:
"Einfluss der Migration auf ein evolutionäres Nahrungsnetzmodell in einer Kette von Habitaten"

Research assistant at TU Darmstadt

2014/15 Tutorial class on "Complex Dynamical Systems"

2014 Lectures: "Introduction to Theoretical Physics" (as stand-in for Prof. B. Drossel)

2013/14 Tutorial class on "Classical Mechanics"

2013 Seminar assistant "Theory of networks"

2012/13 Tutorial class on "Electrodynamics"

2012 Tutorial class on "Methods of Computation in Physics"

2011/12 Tutorial class on "Classical Mechanics"

Publications

In peer reviewed journals

2015 **KT Allhoff, EM Weiel, T Rogge and B Drossel**:
"On the interplay of speciation and dispersal:
An evolutionary food web model in space."
Journal of Theoretical Biology, Volume 336, Pages 46-56.
doi:10.1016/j.jtbi.2014.11.006

2013 **KT Allhoff and B Drossel**:
"When do evolutionary food web models generate complex networks?"
Journal of Theoretical Biology, Volume 334, Pages 122-129.
doi.org/10.1016/j.jtbi.2013.06.008

2012 **KT Allhoff and B Eckhardt**:
"Directed percolation model for turbulence transition in shear flows."
Fluid Dynamics Research 44 031201.
http://stacks.iop.org/1873-7005/44/031201

Under review

KT Allhoff, D Ritterskamp, BC Rall, B Drossel and C Guill:
"Evolutionary food web model based on body masses gives realistic networks with permanent species turnover."
http://arxiv.org/abs/1409.3373

In preparation

KT Allhoff and B Drossel:
"Biodiversity and ecosystem functioning in evolving food webs"
(in preparation)

Conference Contributions

Contributed Talks

2014 **Workshop: Networks on Networks**
"Evolutionary food web models in fragmented landscapes"
in Göttingen, Germany

MPDE Models in Population Dynamics and Ecology
"Migrate, mutate or die: Evolutionary food web models in space"
in Turin, Italy

2013 **Workshop: Structure and dynamics of meta-food webs**
"Food webs - caught between evolution and extinction"
in Bielefeld, Germany

INTECOL Advancing ecology and making it count
"Realistic networks from a new evolutionary food web model"
in London, UK

DPG Spring Meeting
"A new evolutionary food web model"
in Regensburg, Germany

2012 **Annual Meeting of the Ecological Society of Germany, Austria and Switzerland**
"When do evolutionary food web models generate complex networks?"
in Lüneburg, Germany

Poster

2012 **DPG Spring Meeting**
"Directed percolation model for turbulence transition in shear flows"
in Berlin, Germany

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